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STUDIES ON GRAPTOLITES

II. ON THE DEVELOPMENT AND STRUCTURE OF GRAPTOLITE GENUS *GYMNOGRAPTUS* BULMAN *

Abstract. — This paper describes the astogeny and structure of *Gymnograptus linnarssoni* (Moberg) and *G. retioloides* (Wiman) and also the structure of *Gymnograptus* sp. The material has been etched from erratic boulders of Scandinavian origin, which are of Middle Ordovician age. The systematic position of the genus *Gymnograptus* is discussed.

INTRODUCTION

The here described material was etched by chemical treatment, from five Ordovician erratics, by Professor Roman Kozłowski, Head of the Palaeozoological Laboratory of the Polish Academy of Sciences and of the Warsaw University. It was subsequently handed over to the writer to be studied. The most sincere thanks are here expressed to Professor Kozłowski for entrusting the writer with these valuable fossils, and for the helpful advice and criticism during work on the present paper.

While describing this material the writer kept up a constant correspondence with Dr. V. Jaanusson of Uppsala who was kind enough to send numerous explanations and data concerning the age and morphology of the studied forms. Dr. Jaanusson's remarks and suggestions proved very helpful. The most cordial thanks are here conveyed to him for the holotype of *Gymnograptus retioloides* sent on loan from the collections of the Paleontologiska Institution in Uppsala.

The writer also feels greatly indebted to Professor O. M. B. Bulman of Cambridge and to Dr. I. Strachan of Birmingham who courteously sent replies to all inquiries made during the preparation of the present paper.

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* I. Development and structure of *Pristiograptus gotlandicus* (Perner) — see *Acta Palaeont. Pol.*, vol. IV/1, 1959.

Thanks are also due to Dr. H. Mutvei of Stockholm and Dr. J. Kulczycki of Warsaw for the loan of comparative specimens of *Gymnograptus linnarssoni* from the collections of Naturhistoriska Riksmuseet in Stockholm.

The writer also thanks Mrs. K. Budzyńska for the inking of his pencil drawings, Miss M. Czarnocka and Miss L. Łuszczewska for the photography, and Mrs. J. Humnicka for the English translation of the present paper.

The described and figured specimens are housed in the Palaeozoological Laboratory of the Polish Academy of Sciences and of the Warsaw University.

DESCRIPTIONS

Family **Lasiograptidae** Bulman, 1955 [1]

Genus *Gymnograptus* Bulman, 1953

(Genoholotype: *Diplogratus linnarssoni* Moberg, 1896)

Into this genus, so far held as monotypic, *Climacograptus retioloides* Wiman and the form here described as *Gymnograptus* sp. are included by the writer on the structure of thecae. *Gymnograptus* sp. is close to *Lasiograptus retusus* Lapworth which also seems to belong to genus *Gymnograptus* Bulman.

Gymnograptus linnarssoni (Moberg)

(pl. I, fig. 1, 2; text-pl. I; text-fig, 1-12)

1896. *Diplograptus linnarssoni* Moberg; J. C. Moberg, Geologisk Vägvisare..., p. 17, fig. a-c (footnote).
1913. *Diplograptus linnarssoni* Tullb.; A. Hadding, Undre Dicellograptusskiffern..., p. 48, 49, pl. 3, fig. 13, 14.
1951. *Diplograptus linnarssoni* (Tullberg); J. E. Hede, Boring through Middle Ordovician..., p. 59, pl. 3, fig. 3.
1953. *Gymnograptus linnarssoni* (Moberg); O. M. B. Bulman, Some graptolites..., p. 515-517, pl. 2, fig. 17-22, text-fig. 4.
1954. *Gymnograptus linnarssoni* (Moberg); V. Jaanusson & I. Strachan, Correlation of Scandinavian..., p. 686, text-fig. 1. For further references — V. Jaanusson, Graptoloids from Ontikan and Viruan limestones (Ordov.) of Estonia and Sweden (in print).

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[1] For a similar taxonomic unit A. T. Mu used, prior to Bulman, the name Hallograptidae ("On the evolution and classification of Graptoloids", 1950, Ti-chih-lun-Ping, 15, 4-6, p. 182, in Chinese). The name introduced by Mu is probably unknown to most graptolitologists and hence the present writer retains here Bulman's name which is commonly known and better defined.

Material

Specimens etched from two Ordovician erratic boulders by Professor R. Kozłowski who found them on the seashore at Jarosławiec (the Baltic coast, western Pomerania); these boulders are labelled 0.94 and 0.96.

Boulder 0.94 is an organogenic limestone of light ashy colour, made up of minute shell fragments, probably mainly of brachiopods, also of less abundant echinoderms. The limestone does not contain glauconite. It has yielded one proximal end with thecae 1-2 of both series; one more distal part probably belonging to the central portion of the rhabdosome; a fragment of metasicula with the beginning of th 1^1 and with the bud opening of th 1^2; some fragmentary siculae representing a part of prosicula and the beginning of metasicula. This boulder also contained remains, by Professor Kozłowski identified as: *Rhabdohydra tridens* Kozł. (Hydroida), moreover *Mastigograptus* sp., Hystrichosphaeridae, *Ordovicina* sp. (Foraminifera).

Boulder 0.96 is a limestone with somewhat darker colouration than boulder 0.94. It is likewise made up of shell detritus, and contains no glauconite, but numerous pyrite grains. It has yielded one proximal part with 5 thecae and sicula.

In neither of the two boulders is the described graptolite accompanied by other index graptolites or by shelly fauna.

The state of preservation is on the whole very satisfactory. The periderm is but slightly carbonized, somewhat incrusted by pyrite and readily discolouring to an orange hue. Walls of thecae partly damaged, but by suitable combination of fragmentary specimens it has been possible to analyse the essential structural features.

General characters

A biserial graptolite with thecae displaying slight ventral excavation. Proximal thecae approaching the lasiograptid type, the distal nearly orthograptid. Two first thecae lacking apertural processes, the remaining provided with branching, bi- or trifurcated subapertural spines varying in shape. Sicula with virgella and a dorsal spine. Clathrium well developed; periderm attenuated but not reduced. Ontogeny diplograptid, the 4 or 5 first thecae alternating, the remaining probably forming two independent thecal series, but without signs of peridermal median septum.

The here described specimens seem to be conspecific with forms described by Bulman (1953) as *Gymnograptus linnarssoni* (Moberg). Our specimens apparently differ only in the degree of mutual overlap of thecae and stronger curvature of virgella. These differences are most probably without any taxonomic significance.

Development

Prosicular fragment unknown in any sicula. Fig. 4 shows the preserved prosicular part of sicula concealed by thecae, not permitting to determine the length of the prosicula.

Sicula nearly straight, entire length approx. 1.30 mm. In the apertural part the metasicula strongly expanded, attaining a width of approx. 0.40 mm.

As is shown in fig. 1, virgella sets in at a distance of approx. 0.20 mm from the prosicular aperture (by alternation of fuselli on the zigzag ventral suture). It forms a relatively broad list with traces of spiral coiling in the free part. In a mature metasicula virgella is more or less arcuately curved, measuring approx. 0.32-0.50 mm. The curvature of virgella is subsequently used by th 1^1 which follows the virgella curvature and then grows upwards. The free part of virgella gives the semblance of an apertural spine and strongly protrudes beyond the theca.

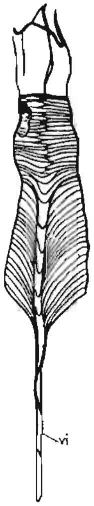


Fig. 1. —*Gymnograptus linnarssoni* (Moberg), young metasicula with preserved fragment of prosicula, *vi* virgella; ca. × 62 (boulder 0.94).

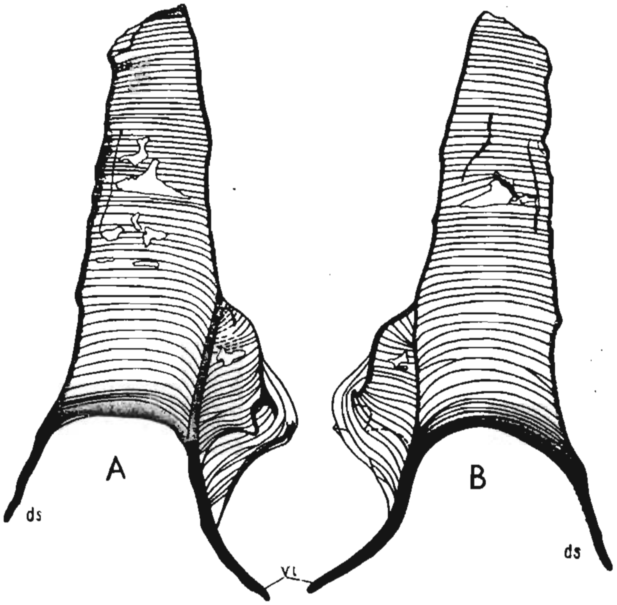


Fig. 2. — *Gymnograptus linnarssoni* (Moberg), metasicula with initial bud and foramen for theca 1^2, *A* reverse side, *B* obverse side; ca × 62 (boulder 0.94).

Metasicula is also provided with a dorsal spine. In mature metasiculae this spine often attains a length of approx. 0.40 mm (fig. 2 *A*, *B*), but is often broken off (fig. 4). Bulman's figure of 0.60 mm, stated for the width of the metasicular aperture, is probably misleading. This is namely (0.70 mm in our specimens) the distance from the base of the dorsal spine to the separation of virgella from wall of th 1^1, while the actual width of the metasicular aperture is approx. 0.40 mm.

The sicula is placed obliquely, at an angle of approx. 160°, to the axis of virgella.

Budding of thecae 1^1 and 1^2. — The next stage of development is represented in specimen shown in fig. 2 *A*, *B*. We can there observe protheca 1^1 and the mode of budding of th 1^2. The initial bud is formed at a distance of approx. 0.25 mm from the metasicular aperture, probably not the definitive one in this specimen. The foramen here is probably initiated by a perforation or resorption. This is suggested by the course of metasicular fuselli in the vicinity of the foramen. At some distance from the beginning of protheca 1^1 a notch is formed within its right wall corresponding to the aperture of bud 1^2. At the same level, in the left wall of protheca, a shield-like expansion with arcuately curved fuselli is formed.

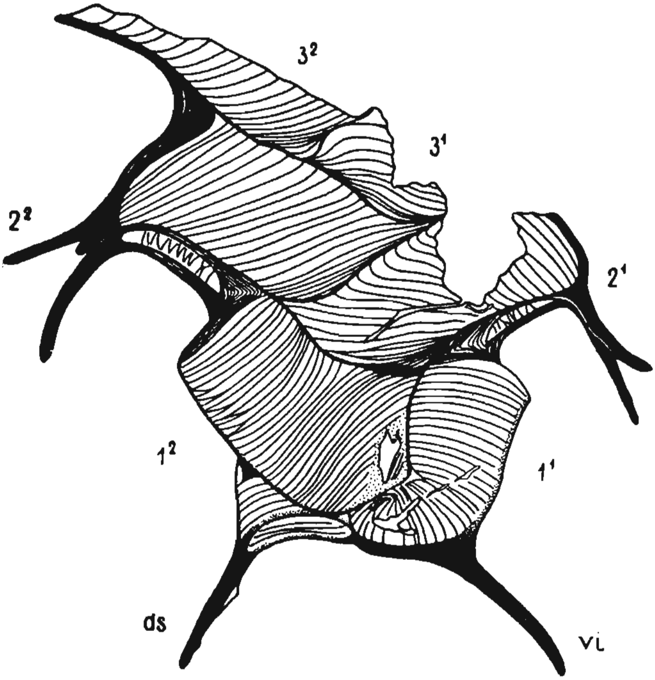


Fig. 3. — *Gymnograptus linnarssoni* (Moberg), fusellar structure of proximal part of rhabdosome, reverse side, *vi* virgella, *ds* dorsal spine; ca × 50 (boulder 0.94).

As is shown by specimens in fig. 3 and 4, with further growth th 1^1

is rather abruptly curved into the shape of the letter J, and agrees in its basal part with the arched curvature of virgella. The arcuately curved prothecal fuselli fill in on the obverse side the geniculate inner concavity of the virgella. Theca 1^1 lacks the true spine whose semblance is given by the virgella extending from the base of that theca. The ventral surface of th 1^1 has a slight curvature and resembles th 1^1 observed in many climacograptids.

The mode of budding in th 1^2 is seen in fig. 3, and still better so in fig. 4. On the reverse side thin fuselli are superimposed in the "knee" angle of th 1^1. They indicate that the growth of th 1^2 is immediately directed upwards, at an angle of about 55° to the axis of virgula. Initially the fuselli are stretched somewhat arcuately, and correspond to the prothecal segment, subsequently the fusellar systems divide to produce metatheca 1^2 and protheca 2^1.

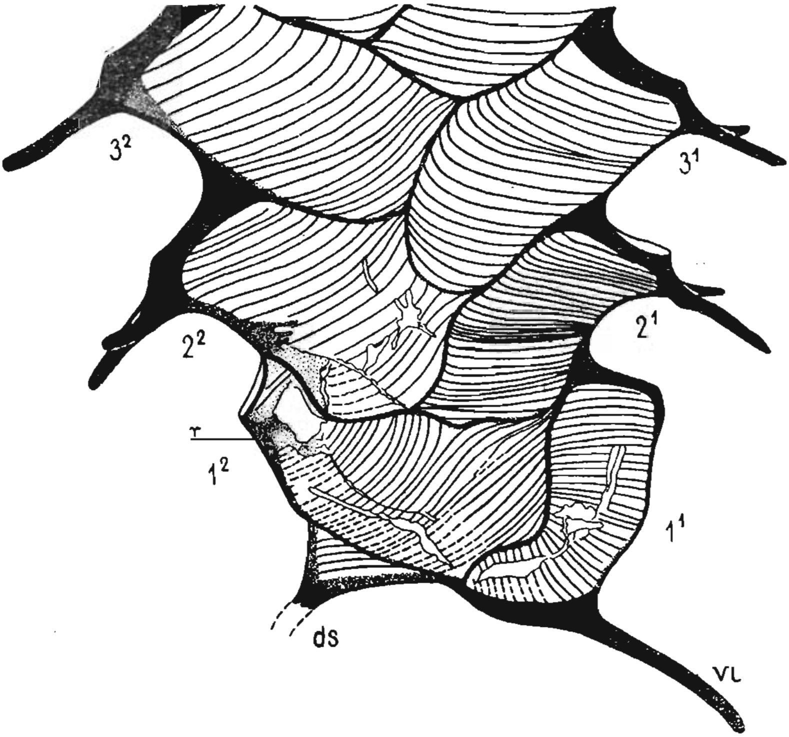


Fig. 4. — *Gymnograptus linnarssoni* (Moberg), fusellar structure of proximal part of rhabdosome, reverse side; *vi* virgella, *ds* dorsal spine, *r* probably regenerated part of thecal wall; ca. × 50 (boulder 0.96).

Theca 1^2, similarly as th 1^1, lacks the apertural spine. A rather small protuberance of th 1^2, by Bulman (1953, fig. 4A, pl. 2, fig. 17) interpreted as the spinal base, may possibly be an artefact (see also photograph in fig. 1, p. 687, Jaanusson & Strachan, 1954).

Budding of thecae 2^1 *and* 2^2. — Theca 2^1 buds from th 1^2. This is suggested by the analysis of the course of fuselli (fig. 3-5) and the direct communication of the interiors of these thecae through an aperture with thickened margin observable in specimen fig. 6*A*. The first fuselli form in the angle between the margin of th 1^1 and protheca 1^2. In one specimen they are notably thinner than the next ones. Gradually they fill in the triangular recess between thecae 1^1 and 1^2. This area is probably the equivalent of protheca 2^1. Then follows the formation of metatheca provided with a paired subapertural spine. On the ventral side occur strongly thickened pleural lists, prolongating then the thickened parietal lists of th 1^1. These lists fuse with the base of the subapertural spines.

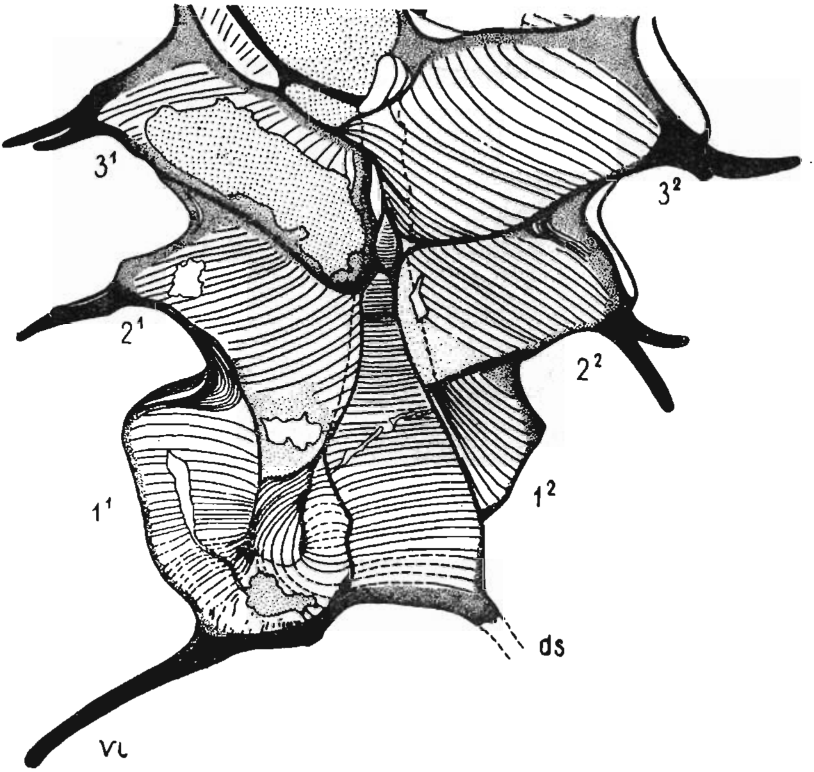


Fig. 5. — *Gymnograptus linnarssoni* (Moberg), fusellar structure of proximal part of rhabdosome, obverse side. Specimen, magnification and explanations — as in fig. 4.

The relations between th 2^1 and th 2^2 require a more detailed description. The fusellar systems of the two thecae are quite independent.

On the reverse side the thecae are limited by a conspicuous thickened list. Nowhere here do we observe intercalations, i. e. wedging in of fuselli of either theca, as is the case in many diplograptids with an aseptal, alternating type of development. On the other hand, however, thecae are strongly obliquely placed to the rhabdosome axis and overlap each other to a considerable extent. The ends of thecae produce a kind of triangular wedge, slightly penetrating into the opposite series of thecae. This might suggest an aseptal alternating type of development. Thus, an analysis of the fusellar structure does not clearly elucidate whether th 2^2 was borne by th 2^1. The solution of this problem calls for an examination of the internal communication between th 2^1 and th 2^2. This is discernible in a transparent and properly oriented specimen in fig. 6*A*. The interrelations of these thecae are diagrammatically shown in fig. 6, 7. The thecae here communicate on the reverse side only, since on the obverse side they do not touch and are separated by a fragment of the free portion of the sicula. In this specimen we may note that the lower part of the distal margin of th 2^1 is provided with a thickened list, slightly protruding inwards. The list forms a large opening probably indicating the way of the budding zooid of th 2^2 when separating from zooid 2^1.

Budding of thecae 3^1 and 3^2. — As previously, the interrelation of the fusellar systems of the two thecae do not clearly indicate their mode of budding (fig. 3, 4). An examination of the connections between the internal cavities of these thecae seems to suggest that they were the first thecae initiating two independent thecal series.

Yet the origin of theca 3^1 is somewhat uncertain. Between the internal cavities of thecae 2^1, 2^2 and 3^1 exists a broad opening, rimmed by thickened list somewhat protruding inwards (comp. fig. 6*A* and 7). This list may be considered as an incomplete, vestigial median septum, which does not occur between further thecae. This opening is broad enough to provide a passage for buds of th 2^2 and th 3^1. It is somewhat difficult to decide whether th 3^1 is borne immediately by th 2^1 — as in the "*teretiusculus*" stage or buds at a small distance from it, from the base of th 2^2 — as in the "*diplacanthus*" stage. The former possibility is suggested by the presence of a small notch in the upper part of opening which may serve for immediate thecal communication between th 2^1 and th 3^1. On the other hand, taking into account the rather advanced mode of budding in the preceding thecae, it is also possible that the bud of th 3^1 is borne at the base of th 2^2. These two possibilities are marked in fig. 8 (the first possibility — by broken lines, the second — by continuous lines).

After examining these two possibilities the present writer is inclined to think that in any case the mode of budding here is somewhat more advanced that in true "*teretiusculus*" conditions (bud of th 3^1 is very close to th 2^2) and perhaps somewhat less advanced than in the true "*diplacanthus*" stage (budding point of th 3^1 somewhat lower). The most objective description of these conditions would therefore be "bud of th 3^1 borne at the base of th 2^2".

Theca 3^2 buds from th 2^2 through a foramen (shown in diagram) rimmed by the abapertural ring. This rather suggests a direct communication of these thecae, similarly as in the septal part of the rhabdosome in many diplograptids.

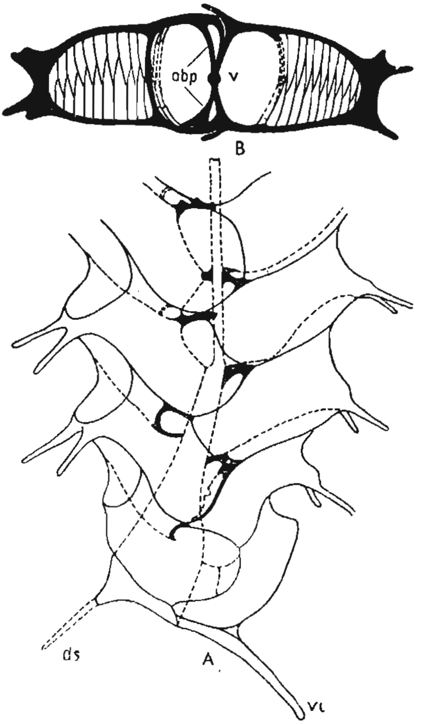


Fig. 6. — Diagram showing borders of thecae and mutual relations of thecae and virgula in *Gymnograptus linnarssoni: A* proximal part of rhabdosome, reverse side; *B* idealized top view of rhabdosome showing relation of virgula to interthecal septa. Borders of thecae visible on opposite side of rhabdosome marked by broken lines; *v* virgula, *abp* abapertural ring, ca. × 25.

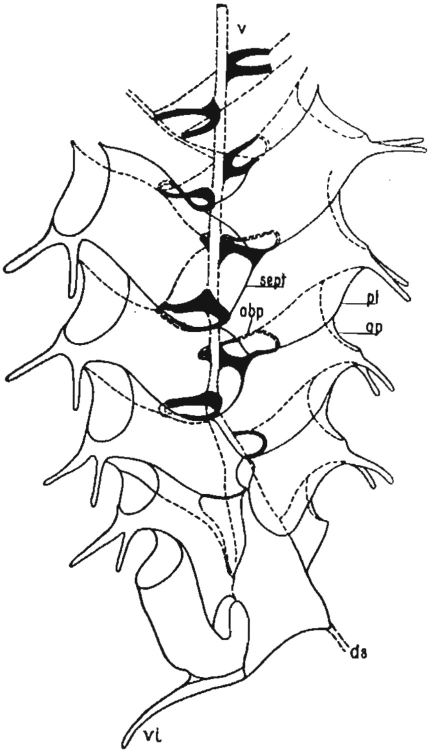


Fig. 7. — Diagram showing borders of thecae and mutual relations of thecae and virgula in *Gymnograptus linnarssoni,* obverse side. Borders of thecae visible on opposite side of rhabdosome marked by broken lines; *v* virgula, *abp* abapertural ring, *ap* apertural list, *pl* pleural lists, *sept* septal lists; ca. × 25.

On the obverse side the walls of th 3^1 and th 3^2 are in contact, enclosing the sicula whose free, visible portion is approx. 0.80 mm.

Budding of the remaining thecae of the rhabdosome. — This is not easily determined with any certainty since *Gymnograptus linnarssoni* apparently represents a rather peculiar type, unknown in literature available to the writer.

He supposes that, beginning with th 3^1 and th 3^2, the development of the rhabdosome rather resembles the septal type (fig. 7). There is, however, no typical septum, i.e. fusellar wall separating the two series of thecae, such as are described in *Climacograptus scharenbergi* (Bulman, 1932*a*) or *Gymnograptus retioloides* in the present paper. The virgula is attached to the parietal lists of thecae by thick peridermal rods, U-shaped, with the opening towards the thecae. These rods perfectly correspond to the incomplete abapertural rings noted in many of the septal forms (fig. 7). We must hence suppose that, similarly as in *Gymnograptus* sp. (see p. 322) described here below, the rod closing up the hollow of the "U" and constituting the edge of the interthecal septum must have been thin and, therefore, destroyed in most cases. It has persisted in th 2^2 only of specimen in fig. 4 and 5, also on one theca of specimen in fig. 9. These facts suggest that *Gymnograptus linnarssoni* is a form whose further development of rhabdosome is of the septal type. The fusellar wall of the septum, however, has disappeared completely, without leaving even a vestigial rib as the one preserved on the obverse side in *Cephalograptus* (Törnquist, 1897, *fide* Bulman, 1932*c*).

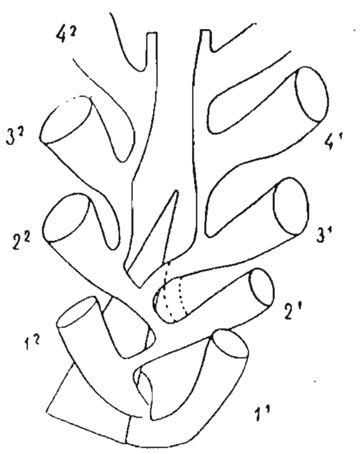


Fig. 8. — Reconstruction of probable mode of development of *Gymnograptus linnarssoni* (Moberg).

The relations in adjacent thecae, absence of the median septum wall excepted, correspond to those noted in septal forms. This is shown by structure of interthecal septum. The interthecal septum is not completely preserved in any of the directly examined thecae; still a close analysis of the edges of the abapertural rods suggests that the septum was started at some distance from the virgula, leaving a free opening for the direct interthecal communication in the two series (fig. 6, 7). In aseptal forms the interthecal septum wall mostly reaches the virgula; its margin is fused with the virgula, so that the adjacent thecae of the particular series are completely separated (comp. *Orthograptus gracilis;* Bulman, 1932*a,* p. 27, fig 14b; *Climacograptus typicalis;* Bulman, 1932*b,* p. 4-6, fig. 2b). In cases where the virgula is not fused directly with the margin of the interthecal septum, it is attached to the lateral rhabdosome walls by short side processes (Cox'es "rods of attachment"; comp. *Climacograptus* (= *Amplexograptus?) inuiti;* Cox, 1933, p. 16, fig. 27). Such structures are regular and their position suggests, as Cox supposes, that they are vestigial abapertural rings. On the other hand, relations noted in *Gymnograptus linnarssoni* fully correspond to those in septal forms: the arrangement of rods is regular while their position agrees with that of the abapertural rings. Moreover, the absence of fusellar intercalations, so characteristic of many aseptal forms (comp. *Orthograptus gracilis, O. apiculatus, Diplograptus leptotheca, Climacograptus* (= *Amplexograptus?*) *inuiti, Diplograptus* cf. *Amplexograptus maxwelli*) suggests that, beginning with th 3^1 and th 3^2, the development of *Gymnograptus linnarssoni* agrees with the septal type.

The lack of the peridermal septal wall is most likely secondary. It is difficult to determine whether its absence is due to inadequate state of preservation. On the whole, however, the thecal periderm is satisfactorily preserved so that it does not suggest accidental destruction of the median septum periderm as an adequate interpretation of its absence. Should this not be so, at least some minute fragments of the periderm would have been preserved on margins of the virgula and of the rods. As it is, these margins are perfectly smooth in all examined specimens, not bearing traces of fusellar periderm. We cannot, however, a priori exclude this possibility, particularly so in view of the very bad state of preservation of the median septum periderm in many specimens of climacograptids. This is observable in numerous specimens of *Climacograptus scharenbergi,* etched from various erratic boulders, which the writer could examine in the collection of Professor Kozłowski. Occasionally, the margins of virgula and of the abapertural rings are extremely smooth. A particularly interesting example is presented in *Climacograptus* sp., etched from the "Schroeteri" Limestone in the island of Öland (loc. Seby) as shown on pl. I, fig. 4. It represents a fragment of the median septum periderm falling out from the thicker peridermal rods enclosing it, so to say "in statu nascendi". The remaining margins will probably have been quite smooth. In such cases, however, a part of thecae retain some traces of the median septum periderm; the falling out of the septum not even leaving vestiges does not seem very likely, independently of the state of preservation.

Much more probable is a conception suggesting that in *Gymnograptus linnarssoni* the peridermal membrane had been reduced during phylogeny. The two thecal series, though budding independently, would not then be separated one from the other by the median septum owing to the disappearance of the peridermal wall. The actual occurrence of such a process is reasonably suggested by the presence in *Gymnograptus* sp. (comp. fig. 18*B*) of a membraneous, strongly attenuated periderm of the median septum. This will be explained by a tendency of the periderm in *Gymnograptus* to attenuation and reduction. This process might actually have begun with the reduction of the median septum. Hence on this evidence we may postulate that:

1) the median septum may have disappeared owing to the reduction of the periderm throughout the septal length;

2) the absence of the peridermal median septum is not always associated with alternating budding, but may occur in septal forms in which the median septum had been subjected to secondary reduction.

So far it was accepted that the reduction of the median septum consists in its progressive abbreviation with simultaneous prolongation of that part of the rhabdosome, where thecal budding is alternating. Morphological data indicate the existence in diplograptids of evolutionary trends characterized by gradual abbreviation of median septum and retardation of its formation (as described by Bulman, 1932*c*, 1936, 1947). This process has been with great lucidity demonstrated by Davies (1929) and more recently by Waern (1948) on a number of forms collected from successive strata. Davies has proved the occurrence of numerous mutations in the evolutionary series of *Glyptograptus persculptus* and *Climacograptus scalaris* from the Upper Ordovician and Lower Silurian in Great Britain. These mutations represent the gradual abbreviation stages of the median septum, and the elongation of part of the rhabdosome with the alternating mode of thecal budding. Waern has confirmed Davies' data for *Climacograptus scalaris* on material from Vestergötland, Kinnekulle. He very thoroughly studied this process which is of undoubt occurrence.

On the base of the above considerations, however, the reduction of the median septum owing to the complete atrophy of the periderm seems probable along with septal reduction through the progressive abbreviation associated with the gradual elongation of the proximal part which displays thecal alternation. The former process is most likely connected with the general tendency to the disappearance of fusellar periderm and may be restricted to graptolite lines displaying this tendency (Lasiograptidae, Retiolitidae).

Virgula and "cryptoseptum"

In *Gymnograptus linnarssoni* the virgula is a relatively strong rod, obliquely placed to the sicula at an angle of approx. 160°. Owing to scarcity of material the writer has not been able to study its microstructure.

Virgula (comp. p. 288) is attached to the rhabdosome walls by incomplete abapertural rings. The general spacing pattern and attachment mode are shown in fig. 6*A* and 7. The relation of the virgula to the links interthecal septum of thecae is given in fig. 6*B*, in which the somewhat idealized relations of two successive interthecal septa are given. The term "*cryptoseptum*" is proposed by the writer for the peculiar type of structure of the median septum with peridermal rods arranged as in septal forms, associated with a lack of the peridermal septal membrane. The presence of two independent rows of thecae, accompanied by absence of the peridermal membrane of the median septum, may be regarded as a major feature "of the cryptoseptal type of development". However, a recognition of this hypothesis calls for more copious material that that available to the writer.

Comparison of development of Gymnograptus linnarssoni with that of other diplogratids

A study of the astogeny of this form, made on material etched from rocks, essentially confirms Bulman's data (1953, p. 516, fig. 4C), based on a careful analysis of forms preserved in relief on the surface of rocks. A comparison of data thus obtained, pertaining to the development of *Gymnograptus linnarssoni,* indicates the diplograptid type of development (fig. 8). This essentially corresponds to the septal type where the first 4 or 5 thecae alternate, while the remaining ones produce two independent thecal series without the peridermal median septum. Th 2^1 or 2^2 gives rise to theca 3^1 (comp. p. 286). If we disregard the lack of median septum, the mode of budding of the first 4 thecae of the rhabdosome exhibits closest analogies with that of *Climacograptus brevis* described by Bulman (1947, p. 62-65, fig. 33 A-C). These resemblances do not concern the general character only, but also some details: mode of budding of th 1^1 is very similar, also the "hood-like shield" produced at the level of the initial bud is likewise noteworthy. Growth direction of th 1^1 corresponds to that noted in *Gymnograptus linnarssoni,* but details of fusellar structure in proximal thecae differ.

The development of *Gymnograptus linnarssoni* differs from that in *G. retioloides* in many respects. Some details of the mode of budding in the first 3 thecae are completely different (comp. fig. 8 and 13), particularly so in th 1^2 and th 2^1. Another difference is the presence in *G. retioloides* of the typical septum which distinctly separates the astogenies of these two species. The astogenetic differences here, however, are not probably more marked than in representatives of many other graptolite genera (comp. p. 326).

Structure of thecae

The fusellar periderm seems somewhat attenuated and thinner than in typical diplograptids. The cortical layer must have been particularly fine, as is shown by the readily discernible fusellar lines. The proximal end of the rhabdosome is on the whole slightly darker than the more distal portion, and this would suggest the presence of a secondary thickening of the periderm.

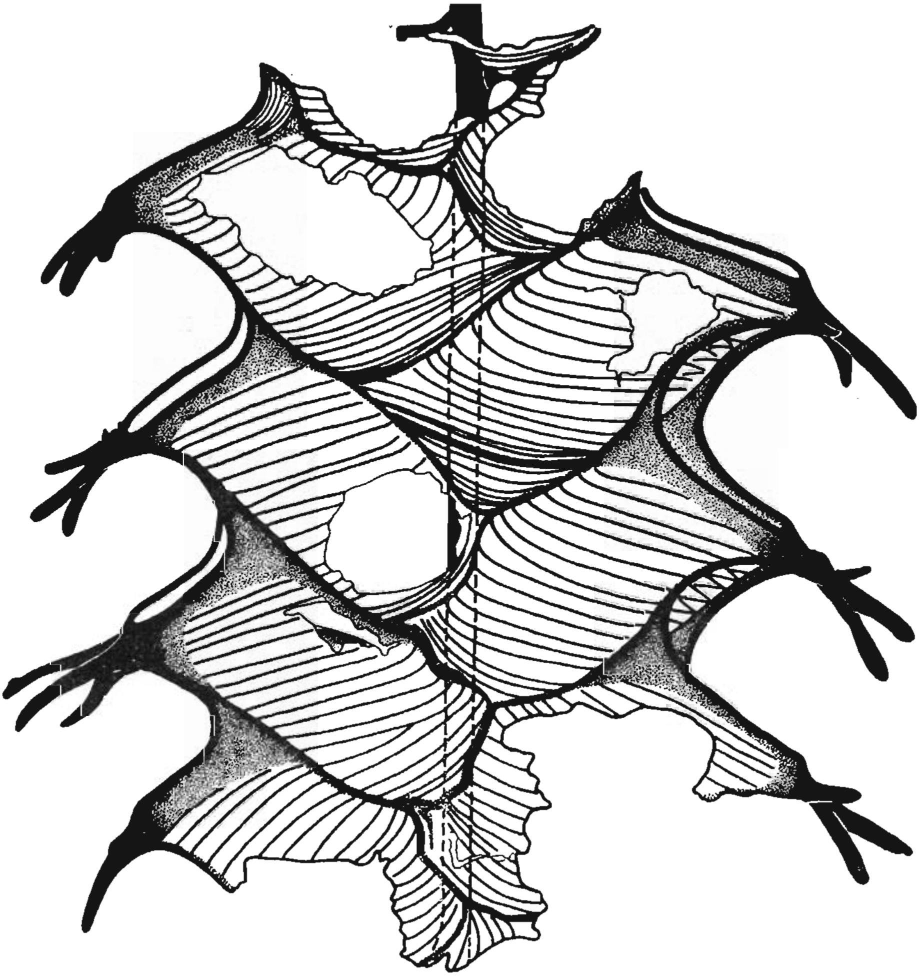


Fig. 9. — *Gymnograptus linnarssoni* (Moberg), more distal part of rhabdosome, lateral view; ca. × 50 (boulder 0.94).

At definite parts of the theca the periderm produces localized thickenings in the form of lists which are a kind of framework for the theca and remind us of conditions in lasiograptids. These thickenings have a laminated structure and are made up of numerous very fine layers of peridermal substance. The bases of apertural processes and the spines themselves exhibit distinctly fusellar structure.

The first 2 thecae of the rhabdosome in *G. linnarssoni* are slightly hooked, being thus nearly climacograptid. They are without spines.

Thereafter the shape of proximal thecae (fig. 3-5) notably resembles the appearance of thecae in lasiograptids, particularly so in shape of apertural region and in position of subapertural processes. The apertural margin, however, is here so to say suspended owing to the presence of secondary structures of the type of angular fuselli. Details of these structures are well shown in fig. 3. They consist of numerous extremely thin growth bands filling in the excavation angle between the apertural margin and the walls of the following theca. In *Gymnograptus retioloides* this corner is filled in by fewer and notably wider angular fuselli of triangular shape (comp. text-pl. VI, fig. 4).

The processes in these thecae are distinctly subapertural, bifurcating at the base or bearing secondary side processes.

The more distal thecae (fig. 9, 10) do not to any considerable extent differ from the more proximal ones. Their excavation, however, is less strongly marked, giving them an appearance of the orthograptid type of thecae. Truly distal thecae, however, are not represented in our material to judge from the width of the preserved part of the rhabdosome. This is approx. 1.70 mm, the maximum rhabdosome width in *G. linnarssoni*, after Bulman, being 2.5 mm. Thecae of this median part are inclined to the axis of the rhabdosome at an angle of approx. 50-55°.

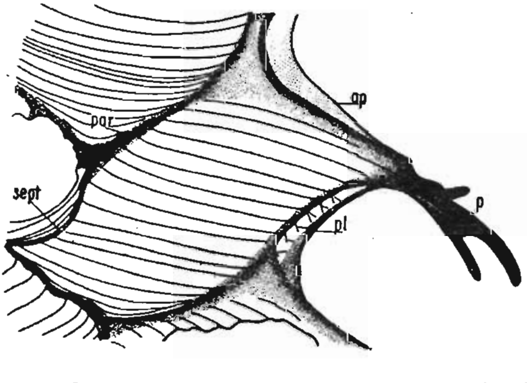


Fig. 10. — *Gymnograptus linnarssoni* (Moberg), fusellar structure of a more distal theca, specimen — as fig. 9 and pl. I, fig. 2; *ap* apertural list, *p* subapertural process, *par* parietal list, *pl* pleural list, *sept* septal list; ca. × 58 (boulder 0.94).

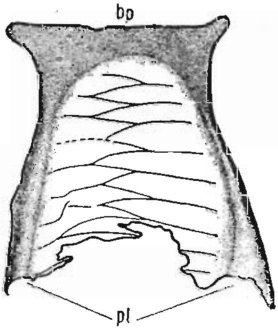


Fig. 11. — *Gymnograptus linnarssoni* (Moberg), fusellar structure of ventral wall of theca; *bp* base of subapertural processes, *pl* pleural lists; ca × 92 (boulder 0.96).

The fusellar structure of thecae is shown in fig. 9 and 10. The theca is formed by the superimposition of fuselli in the corner between two adjacent thecae. At the base it forms a widening passing into the opposite series, owing to which there is strong thecal overlapping. The ventral wall, more or less excavated, is flat, rimmed by two pleural lists with a median zigzag suture (fig. 11).

Measurement data contained in tables 1 and 2 are given to illustrate the development of the rhabdosome.

Table 1

Gymnograptus linnarssoni (Moberg)
Width of rhabdosome, without processes (in mm)

Between thecae	Width
1^1-1^2	1.08
2^1-2^2	1.32
3^1-3^2	1.60
4^1-4^2	1.72
5^1-5^2	ca. 1.84 (damaged)

Thickening of thecal margins. — Margins of thecae are in *G. linnarssoni* rimmed by thickened lists, forming the "clathrium" which is a peridermal framework consisting of strengthening rods.

Table 2

Gymnograptus linnarssoni (Moberg)
Distance of apertures of adjacent thecae (in mm)

Series and thecae	Distance
I. 1-2	0.40
2-3	0.40
3-4	0.56
4-5	ca. 0.60 (damaged)
II. 1-2	0.40
2-3	0.44
3-4	0.56
4-5	0.56

A typical theca (fig. 10) exhibiting the structure of the septal portion of the rhabdosome, is with a clathrium consisting of (comp. fig. 6, 7): 1) apertural list (*ap*), connected with the thickened base of the subapertural process; 2) abapertural ring here incomplete, in the shape of a horse-shoe or of the letter U (*abp*); 3) pleural lists (*pl*); 4) parietal lists (*par*) prolonged into pleural lists of the following theca and fused with the abapertural ring of the theca; 5) additional septal lists (*sept*), less thickened than those previously mentioned and with strongly zigzag course.

The borders of the first 3 proximal thecae are also thickened. Ventral and parietal lists are present on thecae 1^1 and 1^2. Strong septal lists are marked between th 1^1 and th 2^1, also between th 2^1 and th 2^2. On the reverse side, between th 2^1 and th 2^2 they form a broad list arcuately protruding into the interior of the rhabdosome (fig. 6*A*). The edges of this list are strongly thickened. It leaves sufficient space for the bud (comp. p. 286). It may be interpreted as the vestigial median septum.

Structure of subapertural processes. — In all the examined specimens the spines occur below the apertural margin and are, therefore, reasonably called subapertural. However, in agreement with Bulman's opinion (Bulman, 1953, p. 516), they probably become truly apertural in distal thecae. A diagrammatic drawing of the onset of a spine in a young theca is given in fig. 12. It shows that the spine has a fusellar structure and that its base is formed by the superimposition of wide fuselli. The following spines are formed similarly by the superimposition of arcuately curved fuselli onto the base of the process.

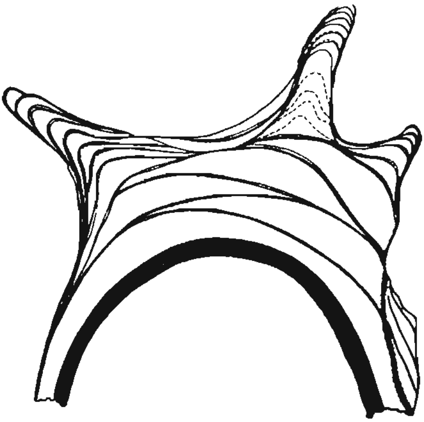
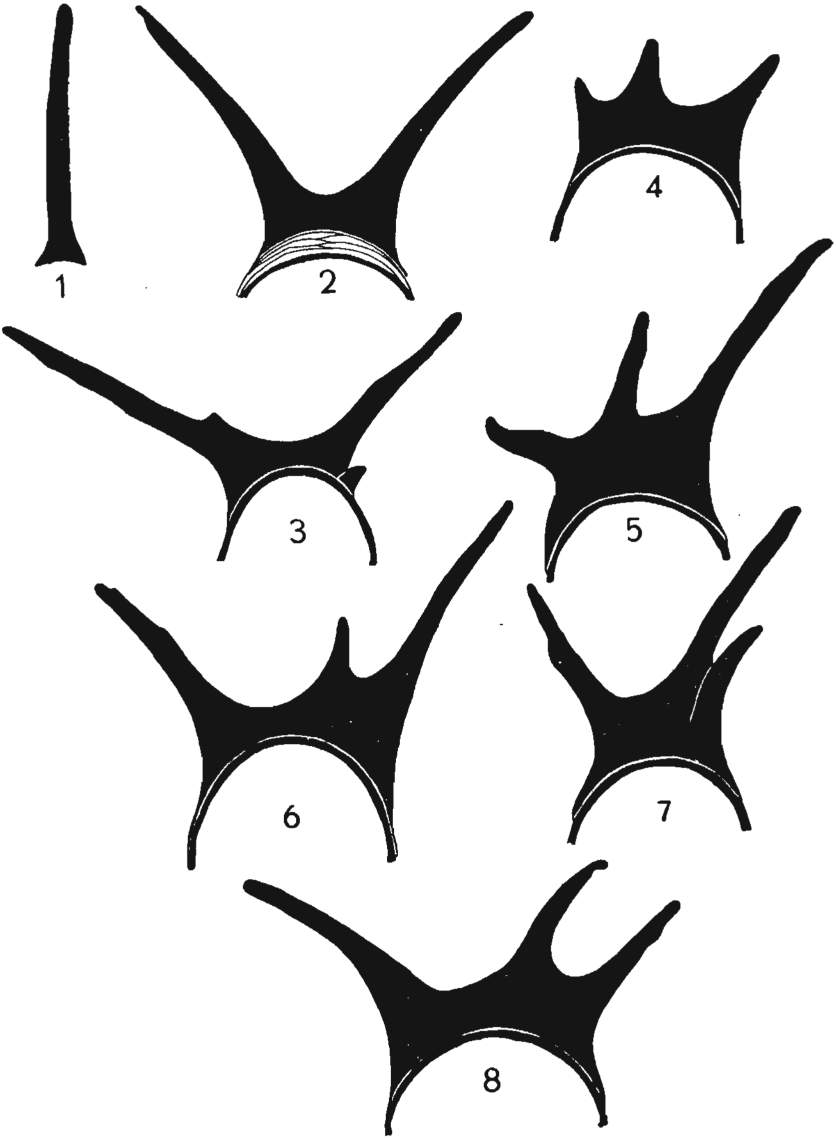


Fig. 12. — *Gymnograptus linnarssoni* (Moberg), fusellar structure of basal part of a subapertural process, simplified, reconstructed parts marked by broken lines; ca. × 116 (boulder 0.94).

Thecae 1^1 and 1^2 are not provided with spines (comp. p. 284). In the following thecae spines are paired, i. e. they are as a rule bifurcated (text-pl. I, fig. 2, 3). One of the rhabdosomes (fig. 4, 5) has the first 5 thecae of each series provided with uniform bifurcated spines; in another rhabdosome a smaller third "budding" spine occurred in addition to two normally developed ones. The more distal fragment exhibits a great variability in the shape of spines, as is shown in text-pl. I, fig. 4-8.

Great variability in the shape of spines and the various number of their bifurcations seems to be a characteristic feature of the studied species. This supposition is confirmed by the information of Dr. V. Jaanusson, who has sent the present writer the following remarks regarding his specimens: "The subapertural spines of *Gymnograptus linnarssoni* are commonly median and single, but curiously enough, in all specimens some of the proximal spines are bifurcated. This bifurcation does not appear to be a consistent feature: it may be present in some thecae of one row of

Text-Pl. I



Gymnograptus linnarssoni (Moberg), variation in the shape of subapertural processes; *1-3* in proximal thecae: *1* free part of virgella, *2, 3* processes in thecae 2^1 and 2^2; *4-8* in distal thecae: *4* onset of a subapertural process; ca. × 76 (boulders 0.94 and 0.96).

thecae. Further, the shape of the bifurcated processes is highly variable, from a blunt process on the side of the otherwise normally developed median spine to a pair of spines of about equal length. As a rule, the bifurcation affects only a few thecae in each rhabdosome" *(in litt.)*.

During the astogeny, the spines on processes in the examined specimens increase from 0.30 to approx. 0.40 mm in length.

Stratigraphic range and geographic distribution

Gymnograptus linnarssoni is known from Middle Ordovician strata of Baltoscandia and from Scandinavian erratic bouldes collected in Poland.

In Sweden it has been recorded from Scania (the Fågelsång district, A. Hadding, 1913; J. E. Hede, 1951). Hede has studied its stratigraphic range on samples of bore cores, determining the *Diplograptus linnarssoni* horizon (Lower *Dicellograptus* shales) as has also been ascertained by Tullberg. He has described this species in a rich faunal association (Hede, 1951, s. 58-60) proving that it passes into the higher "*Climacograptus putillus*" horizon (= *Climacograptus putillus* Hadding, non Hall = *Cl. haddingi* Glimberg). In this horizon this form is still fairly abundant. Hence, it seems more correct, following Jaanusson and Strachan (1954, p. 689), to regard *Gymnograptus linnarssoni* as a characteristic fossil for the *Glossograptus hincksi* subzone, and for the lower part of the *Climacograptus haddingi* subzone in Scania, i.e. for the lower part of the *Glyptograptus teretiusculus* zone (the lowermost Llandeilo s. str.). The stratigraphic range of this species is similar in the remaining areas of Baltoscandia.

According to Jaanusson (1959, in print), outside of Scania this species occurs inter alii in Vestergötland, in the Siljan and the South Bothnian districts, also in erratic boulders with an ostracod fauna, suggesting the Uhaku Stage (= *Cl. haddingi* subzone), as well as in boreholes in the island of Gotland.

In Norway this species is recorded from outcrops in the Oslo district. In Jaanusson's opinion, specimens described by Bulman (1953) seem to come from the same area and would thus correspond to the 4aα_4 — *Trinucleus bronni* beds, equivalent to the *Cl. haddingi* subzone.

In Esthonia this form has been found (Öpik, 1927, 1928; Jaanusson & Strachan, 1954) in the vicinity of Tallinn, Lasnamägi, in the Uhaku Stage horizons (equivalent of *Cl. haddingi* subzone), lately also in the somewhat lower Lasna Stage horizons, an equivalent of the *Glossograptus hincksi* subzone (Obut, 1958, p. 14; Jaanusson, 1959, in print).

No index forms have been found in the fauna yielded by the here mentioned boulders which would provide supplementary data on their stratigraphic and geographic origin. Most likely they were brought from Sweden, and "Crassicauda" or "Schroeteri" Limestone must have been their original matrix.

Gymnograptus retioloides (Wiman, 1895)

(pl. I, fig. 3; pl. II, fig. 1-7; text-pl. II-VII; text-fig. 13-17)

1895. *Climacograptus retioloides* Wiman; C. Wiman, Über die Graptoliten, p. 38, 39, pl. 9, fig. 4.

1908. *Climacograptus retioloides* Wiman; C. Wiman, Studien über das Nordbaltische Silurgebiet, p. 121 (no figure).

Material

The here described specimens have been etched from two Ordovician erratic boulders (0.26 and 0.31), collected by Professor M. Różkowska in Czerwonak, a suburb of Poznań. Both these boulders, lithologically identical, are probably fragments of a larger erratic which subsequently broke up into smaller ones.

Boulder 0.26, as well as 0.31, is an organogenic limestone of light ashy colouration, not containing glauconite. The limestone rock contains a small amount of clay substance and a scanty mineral residuum. A bituminous concentration has been observed on the surface of one of the fragments. One fragment yielded a trilobite pygidium, identified by Dr. V. Jaanusson (Uppsala) as *Pseudoasaphus* aff. *limatus* Jaan. Moreover, *Dendrograptus* sp., *Rhabdohydra tridens* Kozł. and *Epallohydra adhaerens* Kozł. have been etched from the same fragment.

Most specimens of *Gymnograptus retioloides* have been recovered from boulder 0.31. It also contains a shelly fauna of more closely indeterminate nautiloids and brachiopods. Of chitinous fossils the writer has encountered Scolecodonta, Chitinozoa, also some fragments of colonies of Hydrozoa described by Professor Kozłowski as *Diplohydra gonothecata* Kozł. and *Palaeotuba dichotoma* Kozł.

Moreover, both these boulders contain scanty remains of *Glyptograptus*; a proximal part of *Glyptograptus teretiusculus* (His.) has been etched from boulder 0.31.

The whole material available to the writer consisted of a score of prosiculae, one beautifully preserved sicula with the first theca, four rhabdosome fragments in the 3-4 thecae stage, seven proximal fragments in a satisfactory state of preservation, three of these nearly complete. Several rhabdosomes were flattened, with the periderm partly decomposed. The remaining ones, however, were exceptionally well preserved. The periderm was not carbonized, coloured light brown, readily discolouring to an orange tint. It is somewhat incrusted by pyrite.

Diagnosis

Since Wiman's material consisted of one fragment of an uniserial distal part of the rhabdosome only, the main characters of this species are here given in the form of a diagnosis: A biserial graptolite with thecae, of the lasiograptid appearance. First 2 thecae provided with unpaired subapertural spines, the remaining ones with bifurcating subapertural processes in shape of a double loop. Clathrium well developed, periderm thin but not reduced. Diplograptid development of the septal type, with the first 5 thecae alternating.

Distribution. — Erratic boulders of Scandinavian origin. Original matrix probably "Crassicauda" Limestone or the lower "Ludibundus" Limestone of Middle Ordovician age. "In situ" unknown.

Generic position. — Wiman referred this form to genus *Climacograptus* Hall, but here it is provisionally placed in *Gymnograptus* Bulman, which probably better expresses its systematic position.

Gymnograptus retioloides has, so far, been described solely on a single and incomplete specimen, discovered by Wiman in 1892 (loc. Grisslehamn, Wäddö), hence its morphology had not been adequately investigated.

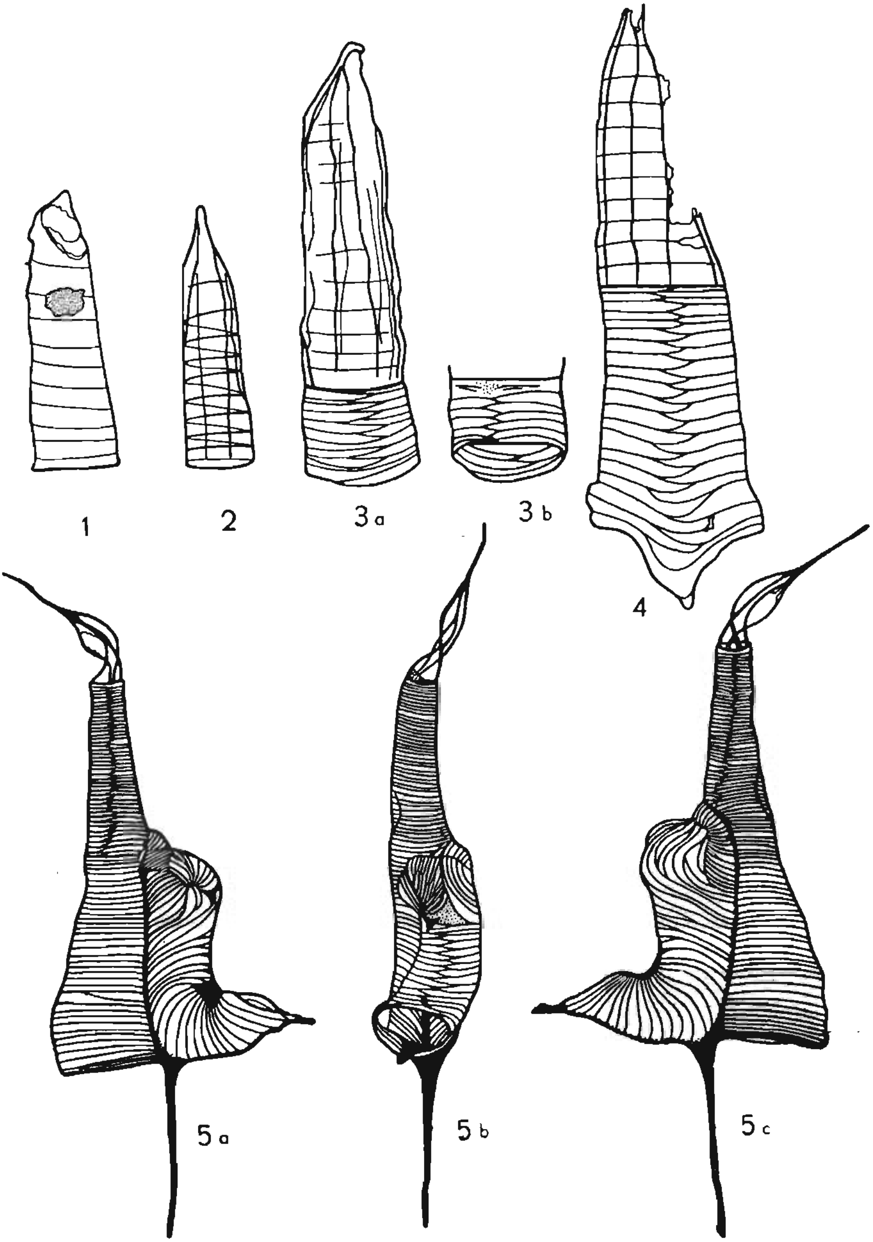
The here described specimens in structure and dimensions wholly correspond to the holotype; they differ in that the membranes of the subapertural spines were missing in Wiman's specimen, while its median septum was satisfactorily preserved.

Development

The rhabdosome originates with the prosicula whose length is 0.36-0.40 mm. In the earliest of the investigated stages (text-pl. II, fig. 1) the prosicula is provided with the helical line only. Its tip is damaged, hence its structure cannot be investigated. In a more advanced stage (text-pl. II, fig. 2) the prosicula is provided — besides the helical line — also with 4 longitudinal ribs. The tip of the prosicula is here present, but the nema has not developed yet, and the ribs do not apparently reach to the very tip. The prosicular aperture is approx. 0.08-0.12 mm in diameter. It is provided with a faintly marked apertural ring, missing in some of the other specimens.

The first fuselli of metasicula are shown in text-pl. II, fig. 3. The virgella which has been formed on the zigzag ventral suture owing to local thickening of fuselli (text-pl. II, fig. 4), originates at a distance of approx. 0.20-0.30 mm from the aperture of prosicula, the list becomes

Text-Pl. II



Gymnograptus retioloides (Wiman), development of sicula and budding of first theca: *1* prosicula without longitudinal threads, ca. × 95; *2* prosicula with longitudinal threads, ca. 95; *3* young metasicula visible from both sides (*a*, *b*), ca. × 125; *4* basal part of virgella, ca. × 145; *5* sicula with first theca, *a* reverse side, *b* ventral view, *c* obverse side, ca. × 47,5 (*1-3* boulder 0.26, *4-5* boulder 0.31).

more thickened at 0.40 mm from the prosicular aperture. The mature metasicula is in measured specimen approx. 1 mm long. The definite metasicular aperture is provided with the virgella only, the dorsal lappet or spine being here missing. The long apertural axis of metasicula is 0.24-0.28 mm. The virgella initially protrudes considerably beyond the apertural area, attaining a length of 0.50 mm. However, in most of the older rhabdosomes it is probably broken off, being only 0.25 mm long. The sicula is straight, with length ranging from 1.12 to 1.40 mm. The prosicula of older siculae is provided with strong virgula.

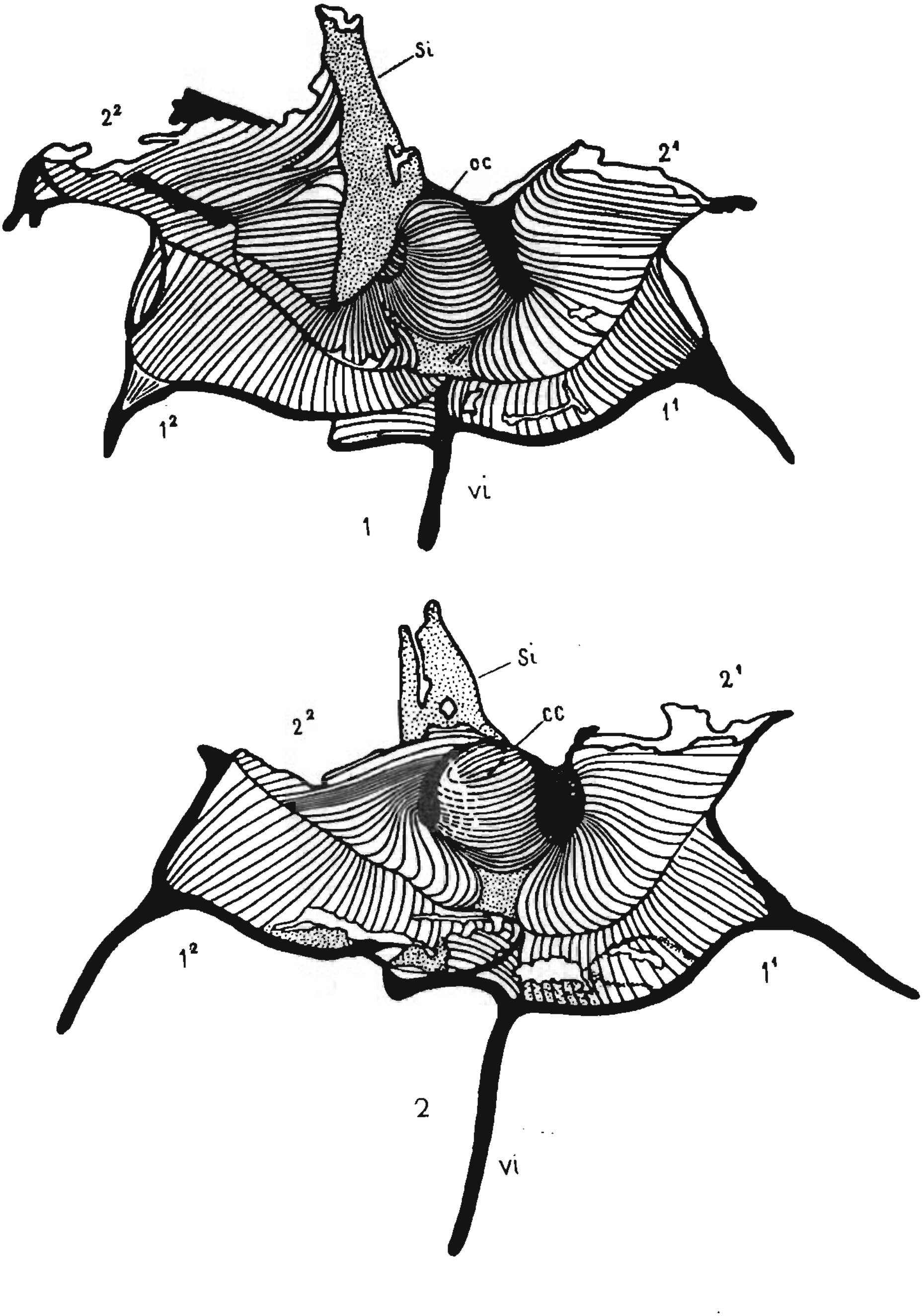
The sicula bearing the first theca of the rhabdosome (text-pl. II, fig. 5) is remarkable owing to the complete lack of the membraneous prosicular wall. The prosicula is represented by 4 longitudinal rods only, at the tip fused into the nema. This makes the relations here similar to those in the regenerative nema, described in many representatives of diplograptids and monograptids (Eisenack, 1941; Urbanek, 1953, 1958). Here, however, the disappearance of the membraneous prosicula cannot be explained by the old prosicula being broken off or damaged, since small fragments of the membrane have persisted near to the tip of prosicula. Hence, the nema here cannot be due to regeneration, while the disappearance of the membraneous wall of prosicula is probably due to resorption. Similar relations have been described by Bulman in specimens of *Cryptograptus bicornis* (Bulman, 1944, p. 30).

Subsequent stages of astogeny may be reconstructed by the analysis of a specimen figured in text-pl. II, fig. 5. Intermediate stages, filling up the gap between specimens in text-pl. II, fig. 4 and 5, were not available to the writer.

Budding of thecae 1^1 and 1^2. — The foramen of the initial bud is formed at some distance from the prosicula (approx. 0.40 mm) to the left of virgella. The arcuately curved fuselli form here a thin thecal tubule, gradually turning to the right and continuing to grow in the plane of symmetry. Further growth of th 1^1 is associated with simultaneous budding of th 1^2. In result the thecal tubule becomes strongly expanded by the superimposition of new notably thicker arcuately curved fuselli (text-pl. II, fig. 5*c*). A shield-like structure is produced at the budding point of th 1^2. On its one side th 1^1 continuing its growth, on the other side (the right) the initial part of th 1^2, laid down in the form of a dome (text-pl. II, fig.5 *a, b*).

Theca 1^1 grows from the very beginning in the direction of the metasicular aperture, down the metasicula wall and then abruptly curving at the level of the metasicular aperture. The proximal and distal portions of theca are here nearly vertical to one another, hence the letter "J" shape of theca. After some time an unpaired apertural spine is formed on the

Text-Pl. III



Gymnograptus retioloides (Wiman): 1, 2 budding of thecae 2^1 and 2^2, reverse side; *cc* crossing canal of theca 2^1, *si* sicula; ca. × 63 (boulder 0.31).

ventral wall of theca (comp. text-pl. VII, fig. 3) and then, with further growth of the aperture, occupies a subapertural position.

Theca 1^2 originates from a number of single fuselli which, over a short distance, are arranged in a pattern suggesting brief initial upward growth (text-pl. II, fig. 5*b*). The fuselli then form a zigzag suture, while the theca gently curves to the right and downwards abruptly to curve upwards on reaching the level of the metasicular aperture. It is, therefore, sigmoidal. This theca is likewise provided with an unpaired apertural spine (text-pl. VII, fig. 4).

The triangular area between the shield-like structure of the initial bud and thecae 1^1 and 1^2 is covered by structureless peridermal membrane (text-pl. II, fig. 5*b*).

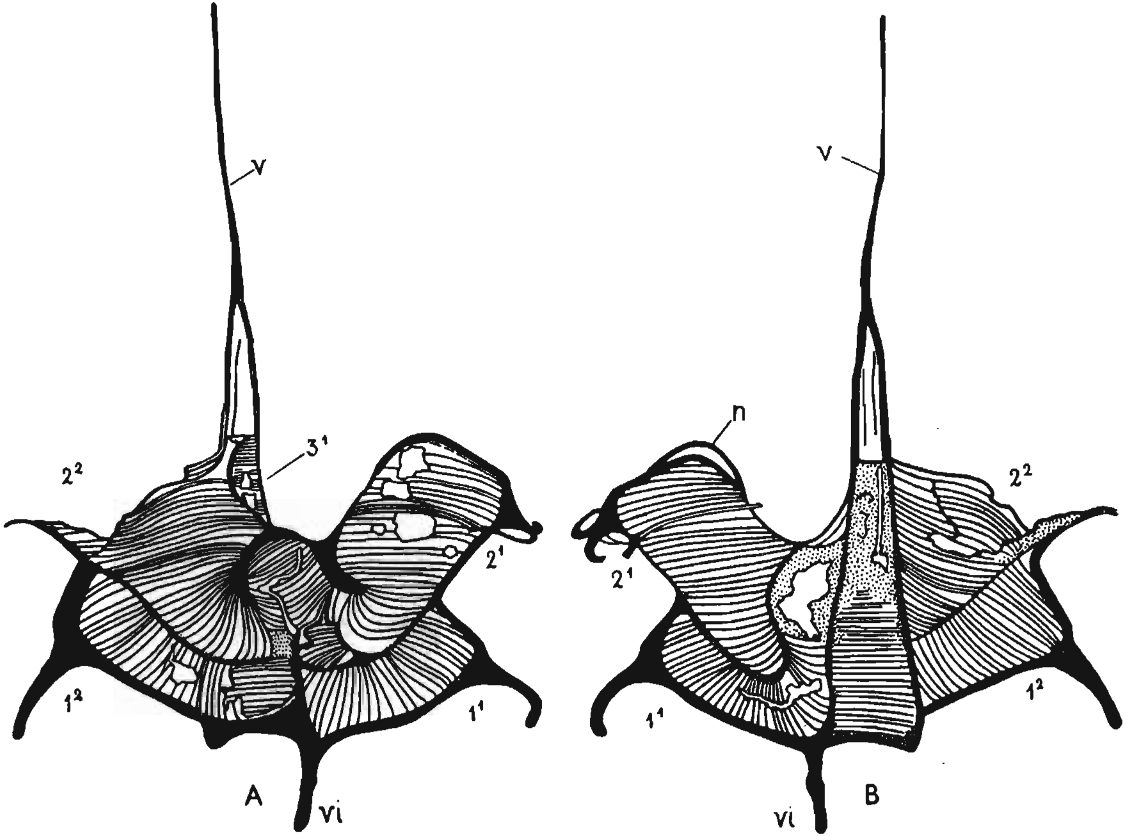
Budding of thecae 2^1 and 2^2. — Subsequent budding of proximal thecae is shown on specimens in text-pl. III, fig. 1, 2. The rather small notch on the margin of the hood of th 1^2, discernible in specimen figured in text-pl. II, fig. 5*b*, probably corresponds to the opening for the crossing canal of thecae 2^1 and 2^2. The walls of this canal (*cc*) are made up of numerous minute fuselli. They are here particularly close spaced and arcuately stretch from the apertural margins on th 1^2 to the strong lateral thickenings, which have a nodular character (text-pl. III, fig. 1, 2). The shape of fuselli suggests that the crossing canal grows quite straight downwards to bifurcate after about 0.20 mm into laterally directed prothecae 2^1 and 2^2. On the whole, the crossing canal is in the shape of a helmet or hood. The free area between the fusellar edges of the crossing canal and those of prothecae 2^1 and 2^2 is filled in by a structureless peridermal membrane. The arrangement of fuselli in this part of the rhabdosome is somewhat peculiar: in shape it rather resembles the letter V or Y (text-pl. III, fig. 1, 2), indicating the limits between fuselli of the crossing canal and those of both prothecae.

Thecae 2^1 and 2^2, initially horizontal, very soon modify their growth direction and are laid down upwards. They are then provided with bifurcated subapertural spines, occurring in all the following thecae.

Budding of thecae 3^1 and 3^2. — Thereafter the budding process displays slightly more peculiar character. Th 2^1 remains "barren", i.e. it does not produce any subsequent theca, while both th 3^1 and th 3^2 are borne by th 2^2. This is indicated by an analysis of the fusellar structure and the mutual relations of these thecae (text-pl. IV and V).

The branching of thecae occurs at a distance of approx. 0.40-0.50 mm from the base of theca 2^2. The fuselli stretched between the distal margin of th 1^1 and th 2^1 bifurcate (text-pl. IV, fig. *A*), because the following ones become attached much higher up on the sicula. A wide opening is formed for the bud of th 3^1. After some time (5-6 fuselli) th 3^2 is initiated as a bud

Text-Pl. IV



Gymnograptus retioloides (Wiman), young rhabdosome in four thecae stage: *A* reverse side, *B* obverse side; *n* notch for interthecal septum of theca 3^1, *v* virgula, *vi* virgella; ca. × 50 (boulder 0.26).

and then the foramen is closed by the formation of the distal wall of metatheca 2^2. Both th 3^1 and 3^2 are from the beginning directed upwards.

There is some uncoformity in the fusellar systems of th 2^2 and th 3^1, the free space between them is filled in by a structureless peridermal membrane (text-pl. V, fig. *A*).

From the attachment place of fuselli, closing up the foramen for the bud of th 3^1, the median septum begins, thereafter stretching between the right and the left row of thecae. On the obverse side the septum is formed between th 4^1 and th 4^2, i.e. from the tip of prosicula. Thecae 4^2 and 4^1 already belong to the septal part of the rhabdosome and they originate from the preceding theca of the same series. Thereafter all thecae are provided with a well marked abapertural ring which constitutes a thickened subquadrate list rimming the foramen of the young bud.

To summarize the here described development of *Gymnograptus retioloides*, it may be stated that this is a diplograptid septal type in which the first 5 thecae alternate, while th 2^2 initiates both th 3^1 and th 3^2. The septum begins on the reverse side between th 3^1 and th 3^2.

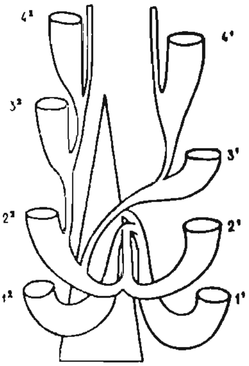


Fig. 13. — Diagram showing mode of development of *Gymnograptus retioloides* (Wiman).

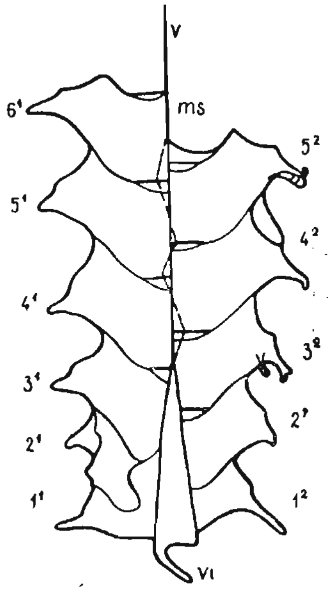
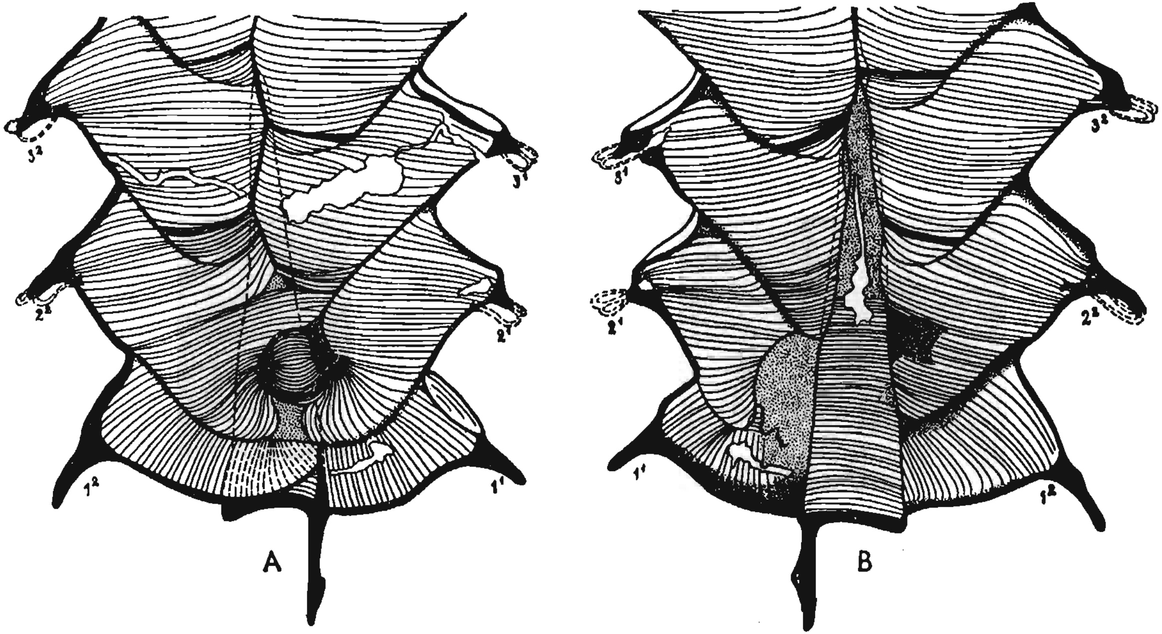


Fig. 14. — Diagram showing the rate of budding in first and second series of thecae in *Gymnograptus retioloides* (Wiman); *v* virgula, *vi* virgella, *ms* median septum. Based on specimen pl. I, fig. 3.

General thecal relations in the proximal part of the rhabdosome and their mode of budding are shown in the attached diagram (fig. 13).

The budding of distal thecae and its "rhythm" is illustrated in fig. 14 and pl. I, fig. 3. The first thecal series always precedes the second series by one theca: when th n^1 is initiated, the formation of theca $(n-1)^2$ is only

Text-Pl. V



Gymnograptus retioloides (Wiman), fusellar structure of proximal part of rhabdosome, somewhat idealized; reconstructed parts marked by broken lines: *A* reverse side, *B* obverse side; ca. × 50 (boulder 0.31).

just commencing. Hence, the median septum is made of thecal walls of the first series, which well explains its single nature (since it is made up of one layer of fuselli only). According to Wiman (1895, p. 38) the distal thecae exhibit a tendency to eliminate differences in the rate of budding of the first and second series, gradually to attain the same level. Owing to inadequacy of material the present writer was unable to check up this process.

Comparison of development of Gymnograptus retioloides with that of other diplograptids

The development type observed in *G. retioloides* cannot be ranked with any of the standard stages of development, determined for diplograptids by Bulman (1936, p. 6-10). It is characterized by a combination of the primitive mode of budding in th 1^1 and th 1^2, also in th 2^1 and th 2^2 — proper for the "*dentatus*" stage (*Glyptograptus dentatus*), with the notably more progressive mode of development of two series of thecae beginning with th 2^2 — proper for the "*diplacanthus*" stage (*Climacograptus diplacanthus*). Though the budding of the first 4 thecae corresponds to the "*dentatus*" stage, yet it is characterized by certain peculiarities, such as e.g. close apertural spacing of the bud in thecae 1^2 and 2^1, whose budding almost directly follows one another. The crossing canal of th 2^1 is directed wholly downwards, while the development of th 3^1 and th 3^2 from th 2^2 reminds us of relations in *Cl. diplacanthus* and in *Cl. scharenbergi* from Laggan Burn (Bulman, 1932*a*, 1947, 1953).

This combination of features, relatively progressive and primitive, does not occur in any diplograptids known to the writer. It might serve as a good illustration of the independent rate of evolution of the particular features, probably rather common in graptolite history. *G. retioloides* indicates that the gradual elevation of thecae either could not keep pace or was not — in this evolutionary trend — associated with the increasing number of alternating thecae, as had probably been the case in climacograptids. Hence, on the whole, an increased number of alternating thecae was here associated with a primitive mode of budding of the first 4 thecae [2].

The here described development of *Gymnograptus linnarssoni* differs in a number of features from that of *G. retioloides*. The position of th 1^2

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[2] Processes expressing similar evolutionary independence of characters have been long known (Osborn, Swinnerton); recently, however, de Beer (1954) has interpreted them as an expression of "Watson's rule". This conception has lately been taken up and expanded by Gross (1956).

and the growth direction in the crossing canal of th 2^1 and 2^2 show the most conspicuous differences. It may be stated that, on the whole, the mode of development in *G. linnarssoni* is more advanced. This is also expressed in the supposed lack of the median septum. These differences do not, however, exceed those known in other diplograptid genera.

The development of other lasiograptids is known in *Lasiograptus* (= *Hallograptus?) hystrix* only. In Bulman's opinion (1932*a*, p. 29-31) this is a septal mode of development, since both th 2^2 and th 3^1 originate from th 2^1. It is readily traceable from the *"dentatus"* stage, from which it differs in more horizontal placement of the crossing canal of th 2^1 and th 2^2. However, we do not know whether this type of development is representative for lasiograptids in general, since *L. harknessi* (Bulman, 1947, p. 11), not yet adequately known in this respect, does actually seem to differ in type of development from *L.* (= *Hallograptus?*) *hystrix*.

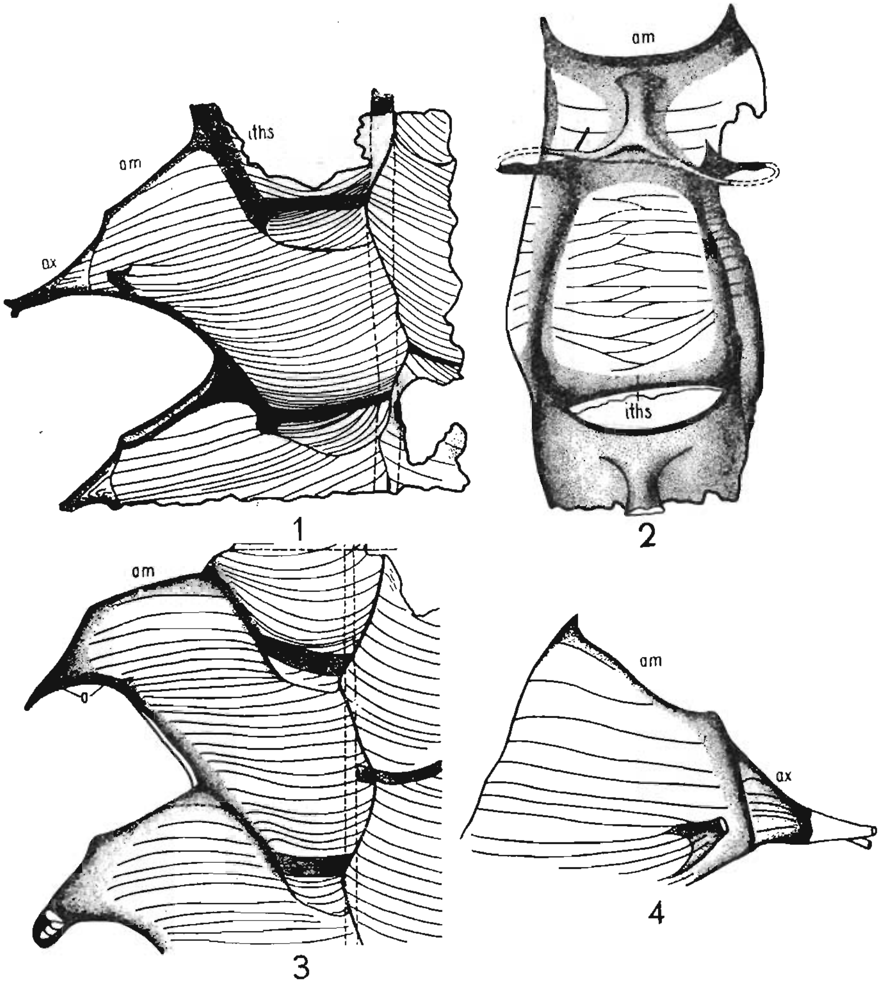
Structure of thecae

Periderm in *Gymnograptus retioloides* is distinctly thinner as compared with that of normal diplograptids, e.g. *Orthograptus gracilis* (Roem.). It represents a thin but still continuous peridermal wall which not anywhere form gaps or openings.

The fusellar structure of the periderm is readily discernible, hence it may be inferred that secondary thickenings, due to the deposition of a cortical layer or of any secondary substance, are not very strong. The slightly darker colouration of the proximal portion of the rhabdosome may be interpreted on the very presence of the thin cortical layer, thicker on the older parts of the rhabdosome. The periderm is not strongly carbonized, light brown, readily discolouring to a light orange tint. Sometimes some nipple-like roughnesses are observable on the surface of the periderm (pl. I, fig. 3). The simplest interpretation of these interesting phenomena is the supposition that they are consequences of some pathological changes of extrathecal membrane affected by diseases or parasites.

Not only the thecal walls, median septum and crossing canals, but subapertural processes too, have a well expressed fusellar structure. Their axial parts consist of several well marked layers which may possibly correspond both to fuselli and to layers of the cortical tissue. The former supposition, however, seems more sound. The membrane stretching between the winged subapertural processes already exhibits a distinctly fusellar structure and consists of a certain number of fusellar bands (comp. text-pl. VII, fig. 1, 2).

Text-Pl. VI



Gymnograptus retioloides (Wiman), fusellar structure of thecae, *1* theca 7^1, lateral view, small fissures of periderm are neglected, ca. × 50; *2* theca showing the structure of ventral wall and interthecal septum, ca. × 98; *3* theca showing the structure somewhat different from that on fig. 1, lateral view, ca. × 50; *4* aperture of theca 6^2 with angular fuselli, *am* apertural margin, *a* arches of processes, *ax* axial part of a process, *iths* interthecal septum, ca. × 90 (boulder 0.31).

It is more difficult to determine the nature of local peridermal thickenings which form the "framework" of the rhabdosome (clathrium). Certain structural details of the ventral list in th 1^1 are shown in textpl. VII, fig. 3. The list consists of a thickening with growth lines, the growth here being probably simultaneous with that of thecal walls. The remaining rods (comp. p. 313) display a layered structure; it is, however, difficult to determine whether they are of fusellar or cortical nature.

Fusellar structure of thecae. — Thecae of *Gymnograptus retioloides* come closest to the lasiograptid type (note especially the presence of nearly vertical thecal wall between apertural border and subapertural process, well visible on text-pl. VI, fig. 1, 3, 4). Proximally, the first thecae do not form a median septum and their structure differs somewhat from that of thecae in the more distal septal part of rhabdosome (comp. p. 311).

Thecae in the septal portion have their first fuselli superimposed in the prothecal corner. These fuselli are short and obliquely arranged. In the basal part the fuselli are occasionally extremely thin and numerous, irregularly arranged. The metathecal fuselli are generally straight. Shorter, intercalated fuselli are sometimes present both in the protheca and in the metatheca, particularly so at the level of subapertural spines (text-pl. VI, fig. 1, 4), and on margins of thecae and of the median septum.

Thecae in *Gymnograptus retioloides* are laterally strongly flattened, hence the rhabdosome section is nearly tabular. The section through the aperture is, therefore, horse-shoe shaped, while that through the abapertural ring is subquadrate (fig. 17*A*). The aperture is with the margin thickened, forming a rod or the apertural list. At the place of attachment to the wall of the next theca the apertural wall is slightly raised and seemingly composed of additional triangular fuselli (text-pl. VI, fig. 4). This shape of aperture is very much like that in *G. linnarssoni* (comp. p. 293). It apparently constitutes that feature in which representatives of *Gymnograptus* differ from those of *Lasiograptus*, where angular fuselli probably do not occur.

Thickenings of thecal margins. — Thecal margins in *G. retioloides* are strongly thickened, with a tendency to form lists producing a clathrium, i.e. a system of peridermal rods.

Transparent specimens of older rhabdosomes show that secondarily thickened lists are formed on the sicula too. A distinct apertural ring is formed rimming the metasicular aperture, while the virgella is thickened. On the reverse side the apertural ring seems to grow thicker than on the obverse side, nearly fusing with the ventral lists of th 1^1 and th 1^2. Two lateral longitudinal rods of the prosicula likewise exhibit a strong thickening (comp. fig. 16).

Thecae 1^1 and 1^2 are provided with an unpaired thickened list stretching from the place of its fixation on the metasicula — to the subapertural spine and connected through it with the apertural list. In specimen figured in text-pl. VII, fig. 3 the ventral list of th 1^1 is shown to form very early as a protruding crest made up of a number of thickenings merging one into the other. The subapertural spine is from the earliest beginning connected with that list.

Thickened parietal lists are likewise formed between th 1^1 and th 2^1, as well as between th 1^2 and th 2^2, subsequently to continue into paired pleural lists of th 2^1 and th 2^2. These lists fuse just below the subapertural spine; through it they are connected with the apertural list which, in turn, fuses with the pleural lists of the next thecae.

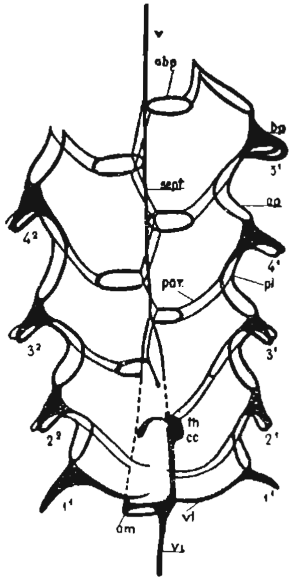


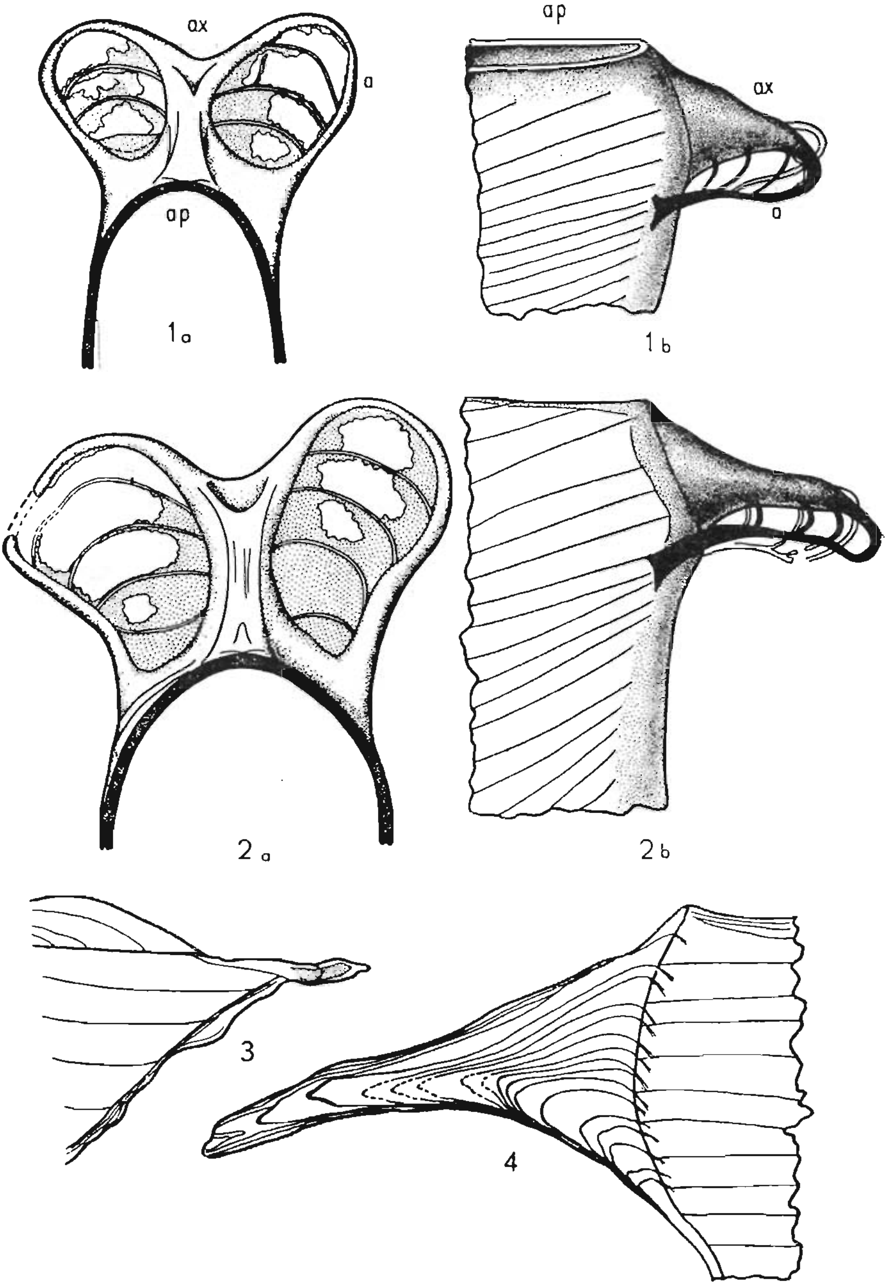
Fig. 15. — Structure of clathrium in *Gymnograptus retioloides* (Wiman), diagram based on a specimen; *am* apertural ring of metasicula, *abp* abapertural ring, *ap* apertural list, *bp* basal part of processes, *par* parietal lists, *pl* pleural lists, *sept* septal list, *th. cc* thickening around the crossing canal of theca 2^1, *v* virgula, *vi* virgella, *vl* ventral list; ca. × 25.

Thecae 3^2 and 4^1 already exhibit a structural type that is common in the septal portion of the rhabdosome. The annexed diagram (fig. 15) illustrates the structural framework of lists forming the clathrium, but without the periderm. That framework is composed of: 1) the apertural list (*ap*), 2) the abapertural ring which is here completely closed (*abp*), 3) pleural list (*pl*), 4) parietal lists which are the prolongation of the pleural lists (*par*), and 5) the septal list (*sept*) less distinctly indicated on the border of the median septum and thecal walls. The septal list has a zigzag course, corresponding to that of septum and is not so well marked as the preceding lists.

Between the pleural lists runs the ventral zigzag suture of the thecal wall (text-pl. VI, fig. 2).

Other localized thickenings of the periderm. — Dark narrow strips of periderm are often noted on thecae. They probably correspond to thickenings bearing the character of thecal rings (text-pl. III, fig. 1, 2) which would be the equivalents of thecal rings in monograptids (Urbanek, 1954, 1958). A ring of this type is particularly well discernible on th 2^2 shown in text-pl. III, fig. 2. These structures seem to be wholly accessory.

Text-Pl. VII



Gymnograptus retioloides (Wiman), structure of subapertural processes, *1* in theca *n* (3 or 4), *a* top view, *b* lateral view, ca. × 115; *2* in theca (n+4), *a* top view, b lateral view, ca. × 115; **3** an onset of subapertural process of theca 1^1, ca × 270 (specimen as in text-pl. II, fig. 5); **4** fusellar structure of subapertural process of theca 1^2, ca. × 270 (specimen as in text-pl. III, fig. 1). (boulder 0.31).

At the level of subapertural spines distal thecae occasionally display a dark strip of periderm, made up of closely set fuselli; this might possibly be associated with arrested growth of the aperture when building up the spine (text-pl. IV).

Subapertural processes. — *Gymnograptus retioloides* is characteristic by peculiar structure of the apertural processes which occur both in proximal and distal thecae slightly below the aperture. They are hence reasonably called subapertural.

The subapertural processes formed in the first 2 thecae of the rhabdosome (th 1^1 and th 1^2) differ in appearance from all the remaining ones. They are namely only single apertural spines (text-pl. VII, fig. 3, 4), similar to the apertural spines in other diplograptids (*Orthograptus*, *Amplexograptus*). Length of the spine here is up to 0.25 mm. Text-pl. VII, fig. 3 shows an onset of spine on th 1^1, consisting of two apposed growth layers laid on the thecal wall as a continuation of the ventral list. The spine grows through the superimposition of successive layers, each one medially thicker. Text-pl. VII, fig. 4 represents the fully developed spine of th 1^2, consisting of 16–17 growth lines, probably the equivalents of fuselli. Since the growth of theca continues sometime after the formation of the processes, the apertural spine becomes subapertural.

The apertural spines on th 2^1 and 2^2, also those in all the succeeding thecae, have a completely different type of structure. When seen from the top, their appearance is that of a double-loop (text-pl. VII, fig. 1, 2). The axial part, after bifurcating, forms two lateral branches. Both branches then curve arcuately and are attached to the thecal wall by their slightly expanded ends below the point of junction with the axial part. These relations are clearly seen in text-pl. VI, fig. 2, and text-pl. VII, fig. 1, 2.

Strongly attenuated fuselli, here forming only a kind of membrane, are spread on the area between the axial part and both arches. On the whole, fragments only of this membrane have been preserved. The fusellar structure of membrane is indicated by fusellar boundaries, preserved as stronger, somewhat ridge-like thickenings. In the corners of the side processes the fuselli are thicker and complete.

The axial part of the process (comp. p. 308) and its arches display laminar structure, visible under strong magnification in sufficiently discoloured specimens. Hence, they resemble the structure of unpaired apertural spines in th 1^1 and 1^2. The continuation of fuselli into the bases of lateral arches (text-pl. VI, fig. 4) suggests the fusellar nature of structure.

The subapertural processes are connected to the thickened apertural ring by a strong thickening of the periderm. On the other side the arches are connected with the pleural lists (text-pl. VI, fig. 2). Hence, the processes are a part of the clathrium.

During astogeny the subapertural processes have a tendency to increase in size in more distal thecae. The length of the basal portion of the spine in theca n ($n = 3$ or 4) is approx. 0.12 mm, while in theca ($n+4$) it is approx. 0.20 mm. Thus, on the whole, they are shorter than the apertural spines of the first 2 thecae.

The here described structure of apertural processes does not meet closer analogies among any other diplograptid apertural processes known to the writer. A resemblance may, however, be pointed out between the structure of apertural spines in *Holoretiolites münchi*, described by Eisenack (1951) and that of the distal thecae of *Gymnograptus retioloides*. The feature that is common to both these forms is the bifurcation of the spine, and the fuselli stretched on it. In *Holoretiolites* they are indicated through fine but distinct rods which constitute the limits of the particular fuselli. The true peridermal membrane has disappeared here completely.

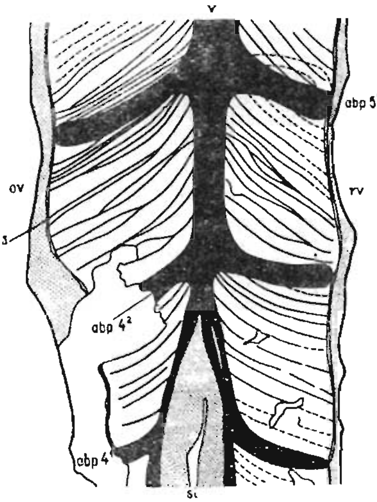


Fig. 16. — *Gymnograptus retioloides* (Wiman), fusellar structure of median septum in theca 4^1; *ov* obverse side, *rv* reverse side, *s* border of protheca and median septum, *si* sicula, *abp* successive abapertural rings, *v* virgula; ca. × 93 (boulder 0.31).

Structure of median septum. — In *Gymnograptus retioloides* the median septum originates between th 3^1 and th 3^2 on the reverse side, and between th 4^1 and th 4^2 on the obverse side. The septum has a zigzag course; it stretches from the abapertural rings of one thecal series to those of the other series. From the abapertural ring of theca n^2 it passes to the abapertural ring of theca $(n+1)^1$. This is a type of septum common in many climacograptids, particularly well known in *Cl. scharenbergi* (comp. Bulman, 1932*a*, p. 9).

The fusellar structure of septum has been examined in a specimen from which one thecal series has been removed, thus giving it a monograptid-like appearance (fig. 16). The septal wall shows the presence of numerous intercalary fuselli; its fusellar structure is irregular. The fuselli are placed obliquely, being raised towards the virgula. The intercalary fuselli occur not only on the surface of the septum, but also on the edge between the lateral wall of protheca and the surface of septum. No traces have been noted by the writer suggesting that the septum is two-layered. This is, however, easily explained by the fact that, during budding, the first series is by one theca in advance of the other thecal series, while the septum is laid down in thecal segments as the dorsal prothecal wall of one series only (fig. 14). The part it plays, as a wall separating the two thecal series, seems therefore secondary. The first fuselli of each successive median septal segment originate simultaneously with the formation of the abapertural ring and the first fuselli of the given protheca.

Interthecal septum. — Thecae 1^1 and 1^2 do not initiate the true interthecal septum, though their distal wall, common to th 2^1 and th 2^2 which are attached to th 1^1 and th 1^2, may possibly be considered as its equivalent. Theca 2^2 already forms a normal interthecal septum, beginning from the abapertural ring of th 3^2, to form a wall common to th 2^2 and th 3^2, and subsequently to continue into the ventral wall of th 3^2. Hence, the interthecal septum is a mixed structure whose initial part constitutes the distal wall of metatheca n, while the next part passes into the ventral wall of theca $n + 1$.

The fusellar structure of the interthecal septum is shown in text-pl. VI, fig. 2. Its relation to the virgula is illustrated by fig. 17*A*. In *Gymnograptus retioloides* the structure is perfectly normal, lacking the intercalary fuselli. The septum passes gradually, without irregularities, into the ventral wall rimmed by pleural rods, medially traversed by a zigzag suture.

Theca 2^2 is characterized by somewhat different relations. In the apertural region (text-pl. IV, fig. *B*) a notch is formed within the distal metathecal wall, rimmed by thickened list on which a kind of interthecal septum originates between th 2^1 and 3^1.

The measurements of the rhabdosome are given on tables 3 and 4.

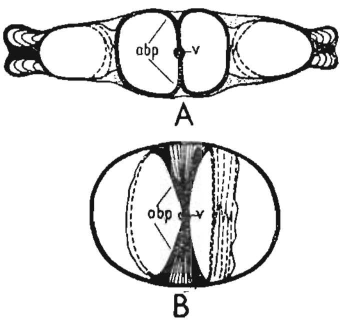


Fig. 17 — *A* idealized cross section of rhabdosome in *Gymnograptus retioloides* (Wiman) based on top view of a rhabdosome, *B* ditto in *Climacograptus* cf. *scharenbergi;* abp abapertural ring, *v* virgula; ca. × 25.

Virgula

In *Gymnograptus retioloides* the virgula originates from the fusion of the longitudinal rods of prosicula (text-pl. II, fig. 5). In the majority of cases we probably have 4 longitudinal rods, merging into the virgula.

The microstructure of nema has repeatedly been the subject of a discussion. The chief problems here are those concerning the laminar structure of the nema, and the question whether it is a solid peridermal thread or a tubule provided with a central canal.

Owing to the adequate state of preservation of *G. retioloides,* the writer was able to prepare thin microtome sections of several fragments of the virgula. Although he did not possess a virgula originating at the apex of prosicula, still on the shape of the section of virgula he reasonably inferred that one of the fragments (pl. II, fig. 4, 5) was more proximal than the other (fig. 6, 7). Plate II, fig. 4 represents a fragment of virgula with distinctly triangular shape. It is reminiscent of Cox's observation (1933, p. 16) postulating a triangular shape of section of the virgula at a certain distance from the prosicula in *Climacograptus* (= *Amplexograptus*?)

Table 3

Gymnograptus retioloides (Wiman)

Width of rhabdosomes, without processes (in mm)

Between thecae	Rhabdosomes		
	I	II	III
1^1-1^2	1.08	1.08	1.08
2^1-2^2	1.20	1.24	?
3^1-3^2	1.24	1.28	1.28
4^1-4^2	1.28	1.40	1.28
5^1-5^2	1.32	1.36	1.36
6^1-6^2	1.32	1. ?	—
7^1-7^2	1.32	—	—

Table 4

Gymnograptus retioloides (Wiman)

Distance of apertures of adjacent thecae (in mm)

Series and thecae	Rhabdosomes		
	I	II	III
I. 1-2	0.48	0.48	—
2-3	0.44	0.40	—
3-4	0.52	0.52	—
4-5	0.56	0.52	—
5-6	0.52	0.56	—
6-7	0.52	0.56	—
II. 1-2	0.52	0.52	0.48
2-3	0.52	0.48	0.48
3-4	0.52	0.52	0.60
4-5	0.52	0.52	0.58
5-6	0.52	0.60	?
6-7	0.60	—	—

inuiti Cox. This shape is by Cox explained by the unsimultaneous disappearance of each of the 4 longitudinal rods of the prosicula. The earlier disappearance of one of the rods imposes a triangular shape to the virgula.

The laminar structure of virgula is readily discernible in microphotographs which likewise clearly show the presence in virgula of *G. retioloides* of an axial canal with the maximum diameter at approx. 0.015 mm. The exterior branches of the triangular virgula are approx. 0.030 mm (pl. II, fig. 4, 5).

Microtome sections of the other fragment of virgula (pl. II, fig. 6, 7) adequately illustrate its laminar growth. The outline of the virgula is irregular, probably owing to an injury of the surface. However, the course of growth lines indicates that the virgula did not thicken quite holoperipherally. The virgula diameter was approx. 0.055-0.057 mm, that of the axial canal — approx. 0.016 mm. The thickness of the particular growth layers ranges from approx. 0.002 to approx. 0.003 mm.

The laminar structure of nema confirms the supposition that, concurrently with R. Kozłowski's views (1948, p. 91), it is a product of extrathecal tissues. Its microstructure, similarly to that of virgula examined in *Cucullograptus pazdroi* (Urbanek, 1958, p. 15) points out to a resemblance with the microstructure of the cortical layer in dendroids (Kozłowski, 1948, pl. 4, fig. 8) at the base of the sicula. Hence a resemblance with the basal disc too. This will be understood on the supposition that both these structures are on the whole homologous.

The presence of a canal in the virgula is probably not a constant feature in graptoloids. Some of them, e.g. Monograptidae, *Corynites*, are not provided with a central canal in the virgula, while in others, e.g. Diplograptidae and related groups, possibly particularly so, the virgula is provided with a canal. This may be an accessory feature, dependent on the tubule diameter of the extrathecal tissues in which the virgula originates. The diameter of the inner canal of the virgula seems to be constant, being approx. 0.015 mm in *G. retioloides.*

The here studied material did not enable the writer to investigate the structure of a young virgula or its formation from the longitudinal rods of prosicula. However, it seems that the connection of the central canal of the virgula with the prosicular cavity — if it did exist as was postulated by Cox (1933, p. 16) — was of a secondary nature. Young prosiculae, still without rods, are apically closed. Moreover, in representatives of numerous diplograptids the presence has been noted of a basal membrane (diaphragm), separating the prosicular cavity from its apex.

Hence, it may be inferred that the growth of virgula is wholly peripheral, external, and that the central canal was not, during the life-time

Table 5

Comparison of *Gymnograptus linnarssoni* (Moberg) and *Gymnograptus retioloides* (Wiman)

Gymnograptus linnarssoni (Moberg)	*Gymnograptus retioloides* (Wiman)
1. Size of rhabdosome probably somewhat larger than in *Gymnograptus retioloides.*	Size of rhabdosome probably somewhat smaller than in *Gymnograptus linnarssoni.*
2. Length of sicula 1.30 mm.	Length of sicula 1.12-1.40 mm.
3. Breadth of rhabdosome (exclusive of apertural processes): at thecae 1^1-1^2 — 1.08 mm, at thecae 4^1-4^2 — 1.72 mm.	Breadth of rhabdosome (exclusive of apertural processes): at thecae 1^1-1^2 — 1.08 mm, at thecae 4^1-4^2 — 1.28-1.40 mm,
4. Sicula inclined at about 160° to the rhabdosome axis.	Sicula in prolongation of the rhabdosome axis.
5. Presence of the dorsal spine in metasicula.	Absence of the dorsal spine in metasicula.
6. Thecae 1^1 and 1^2 without any processes.	Thecae 1^1 and 1^2 provided with simple apertural spines.
7. Subsequent thecae provided with bifurcated or manyfolded, highly variable subapertural processes.	Subsequent thecae provided with subapertural processes in form of double loop and with stable shape.
8. Budding of thecae 1^1-1^2, 2^1-2^2 as in *"diplacanthus"* stage.	Budding of thecae 1^1-1^2, 2^1-2^2 as in *"dentatus"* stage.
9. Theca 3^1 borne at the base of theca 2^2, theca 3^2 borne by theca 2^2	Thecae 3^1-3^2 borne by theca 2^2.
10. Further development probably in two independent thecal series.	Further development in two independent thecal series.
11. Median septum periderm lacking, no traces of it preserved.	Median septum periderm present.
12. Virgula connected with rhabdosome wall through "U"-shaped rods, forming incomplete abapertural rings.	Virgula connected with rhabdosome walls through rods forming complete abapertural rings.
13. Interthecal septa probably leaving a subcircular channel for interthecal communication.	Interthecal septa leaving a subcircular channel for interthecal communication.
14. Thecae with "lasiograptid" appearance.	Thecae with "lasiograptid" appearance.
15. Thecae with somewhat attenuated periderm and thickened lists forming a kind of clathrium.	Thecae with somewhat attenuated periderm and thickened lists forming a kind of clathrium.
16. Septal lists sharply zigzag shaped.	Septal lists midly zigzag shaped.
17. Apertural margin of thecae suspended on the wall of next thecae.	Apertural margin of thecae suspended on the wall of next thecae.

Table 5 (*continued*)

Gymnograptus linnarssoni (Moberg)	*Gymnograptus retioloides* (Wiman)
18. Suspended part of apertural margin consists of very numerous and narrow fuselli.	Suspended part of apertural margin consists of few, short "angular fuselli".
19. Distal thecae inclined at 50-55° to the rhabdosome axis.	Distal thecae inclined at 35-40° to the rhabdosome axis.
20. Cross section of rhabdosome tabular.	Cross section of rhabdosome nearly tabular.

of the animal, filled in by tissues, but that it constituted a hollow rimmed by the first growth ring of the virgula.

The mode of junction of fuselli of the median septum with the virgula is shown in fig. 16. We can also see there the junction of the virgula to the abapertural ring (see also fig. 17*A*).

Generic position

Wiman (1895) when first describing this species, referred it to genus *Climacograptus* Hall. As it is shown above, "*Climacograptus*" *retioloides* is certainly not a climacograptid, since the ventral climacograptid notch of thecae does not occur in this form. Moreover localized thickenings of periderm are developed, forming a kind of clathrium. In this character this form approaches Lasiograptidae Bulman rather than Climacograptinae Frech. The developmental pattern here described for *Gymnograptus retioloides* does not resemble relations in the so far studied climacograptids (comp. p. 307).

In the shape of thecae, cross section of rhabdosome and its general appearance, development of clathrium, pattern of subapertural spines, this species comes closest to some Lasiograptidae. It should be placed therefore in the family Lasiograptidae Bulman, close to *Gymnograptus*. Some similarity in thecal structure and in general appearance of rhabdosome is here undeniable. It is therefore possible formally to place it in *Gymnograptus*. From the genoholotype of this latter it differs, however, in many details of structure and development (comp. table 5). Particularly notable differences occur in features 4-8, 11, 12, 16 (tab. 5). The development of both forms, though diplograptid, differs strongly. Moreover the details of structure of subapertural spines are essentially different. On the other hand, it remains rather obscure how to rank taxonomically differences in the mode of development (comp. considerations, p. 326). The present author has, therefore, decided to place the above described species in genus *Gymnograptus* sensu lato, in order to avoid erection of a new monotypic genus and taking into account some general similarities (comp. tab. 5).

However, from the morphological point of view, the existing differences between the genoholotype of *Gymnograptus* and *G. retioloides* would perhaps sufficiently justify the establishment of a separate subgenus or genus [3], but this latter should be placed into Lasiograptidae, close to *Gymnograptus.* Taking also into account the presence of some forms morphologically intermediate between *G. linnarssoni* and *G. retioloides,* as the here described *Gymnograptus* sp., the writer believes that the best solution is to leave the decision to those in possession of more adequate material. At the present moment the considered form is provisionally placed in *Gymnograptus* on the base of doubtless similarities in some general features of the rhabdosome.

Stratigraphic range and geographic distribution

Gymnograptus retioloides has not thus far been studied from rocks "in situ", but described from erratic boulders only. When describing this form Wiman (1895, p. 38) states that the only specimen "stammt aus einem Geschiebe vom grauen Kalk des Bottnischen Meeres und ist bei Grisslehamn im Kirchspiel Wäddö gefunden". Previously (p. 37) that author mentioned that this limestone probably corresponds to the "Centaurus + Chasmopskalk", but also that the determination of its more exact position calls for further investigation.

In 1908 Wiman reports *Climacograptus retioloides* from an erratic boulders "Höganäs Nr. 10 aus älterem Chasmopskalk" (1908, p. 121) as occurring in the following faunal association (1908, tab. 6): *Phacops exilis* Eichw. (= *Estoniops exilis* (Eichw.), R. Männil, 1957), *Cheirurus* sp., *Remopleurides* sp., *Leptaena oblonga* Pand. — *Estoniops exilis* (Eichw.) has been recorded from the Kukruse Stage in Estonia (Männil, 1957, p. 387) which is the equivalent of the lower part of the "Ludibundus" Limestone of Scandinavia (lower part of the *Nemagraptus gracilis* zone). By the presence of *L. oblonga,* however, a somewhat lower Uhaku Stage is also suggested.

The presence of *Glyptograptus* has been ascertained in boulders studied by the writer: boulder 0.31 has yielded the proximal part of a rhabdosome, probably belonging to *Glyptograptus teretiusculus* (Hisinger). Some caution must, however, be exercised here in regard to specific identification based on one specimen only, owing to the presence of

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[3] Similar opinion was expressed by Prof. Bulman and Dr. Strachan in letters kindly sent to the present writer.

morphological forms intermediate between *Glyptograptus dentatus* and *Gl. teretiusculus* (comp. Bulman, 1936, p. 57), which probably occupy an intermediate stratigraphic position. *Glyptograptus teretiusculus* persists across several graptolite zones (*Gl. teretiusculus* — *Clim. wilsoni,* i.e. from the Llandeilo through the lower Caradocian), but evidence supplied by lithology and the occompanying fossils does not deny that we are dealing here with the *Gl. teretiusculus* zone.

Besides graptolites the present writer has discovered in boulder 0.26 a trilobite pygidium. Dr. Jaanusson was kind enough to identify it as *Pseudoasaphus* aff. *limatus* Jaan. stating that this species "is probably new, though very close to *P. limatus* from the Uhakuan of Dalarna and Oslo region" (personnal communication). According to that information, *Pseudoasaphus* has not been reported in Baltoscandia from beds higher than the lower Kukruse substage (C_{II} α).

According to Dr. Jaanusson, the lithology of that boulder suggests the Uhaku Stage ("Crassicauda" Limestone) as well as the lower part of the Kukruse Stage (the lowermost "Ludibundus" Limestone).

Lithological data and the associated fauna indicate that the most likely horizons from which the here studied specimens of *Gymnograptus retioloides* were derived, are not lower than the "Crassicauda" Limestone (= upper part of *Gl. teretiusculus* zone) and, probably, not higher than the lower "Ludibundus" Limestone (= the lowermost part of the *Nemagraptus gracilis* zone). The "Crassicauda" Limestone is suggested by the presence of *Gl. teretiusculus*, the "Ludibundus" Limestone — by that of *Pseudoasaphus.*

Gymnograptus sp.

(text-fig. 18 *A-C*)

Material. — One specimen, probably a fragment of the median part of the rhabdosome (fig. 18*A*), etched from erratic boulder 0.181 found at the foot of a moraine at Mochty (approx. 40 km NW of Warsaw), in the Vistula valley. State of preservation unsatisfactory, periderm rather strongly damaged, covered by sediment. In order to avoid injury the specimen was not cleared, but the slight degree of carbonization allowed an examination of its main structural characters.

Description. — Thecae lasiograptid (fig. 18*A*), uniting certain structural features of *Gymnograptus linnarssoni* (shape of subapertural processes) with those of *G. retioloides* (general shape of thecae). Theca provided with thickened lists forming the clathrium. This consists of: 1) apertural U-shaped list, 2) pleural lists connected with base of subapertural processes and through them with the apertural list, 3) parietal lists, and 4) abapertural ring. The abapertural ring is not complete; on the specimen it is indicated as a strongly thickened, U-shaped rod basally fused with the virgula. The rod closing up the hollow of the "U" and constituting the edge of the interthecal septum was probably thin, as e.g. in *Lasiograptus harknessi*. Most likely it has been damaged as that in *Gymnograptus linnarssoni*. A fine membraneous periderm spans the pleural lists; the periderm is traversed by a zigzag ventral suture of fuselli.

The median septum extends along a zigzag line, forming on the surface a strongly marked septal list, connected with the other elements of the clathrium. The peridermal wall of the median septum is only fragmentarily preserved (fig. 18*B*). It is a very fine membrane, readily damaged, but its vestiges persist on edges of the virgula, and of the rods of the abapertural rings.

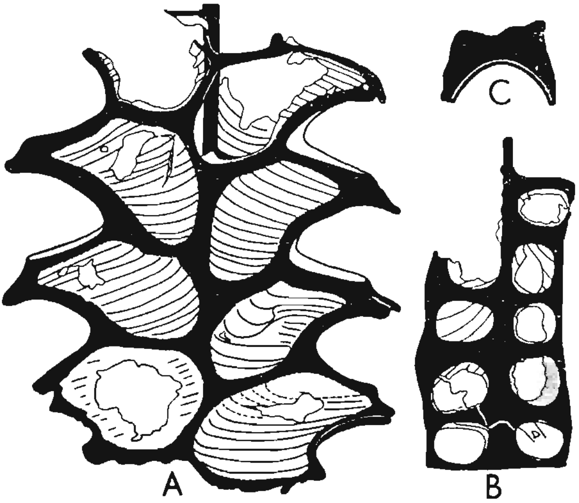

Fig. 18. — *Gymnograptus* sp., *A* fragment of rhabdosome, lateral view, *B* somewhat simplified fragment of median septum, *C* subapertural process, top view; ca. × 25 (boulder 0.181).

Thecae are provided with subapertural processes in the form of a bifurcated spade-like protuberance (fig. 18*C*). They resemble the "onset" or a young process in *G. linnarssoni* (comp. text-pl. I, fig. 4). Here, however, this form may constitute their definite, matural shape. Thecal aperture straight, without angular fuselli.

Comparison. — The structure and dimensions of thecae strikingly resemble those in *Lasiograptus retusus* Lapworth, so much so that they may be conspecific. *Gymnograptus* sp. also resembles a graptolite described by Bulman as a variety of *Climacograptus scharenbergi* (Bulman, 1932*a*,

p. 6, pl. 1, fig. 23-26). In Dr. Jaanusson's opinion (*in litt.*), however, this is a lasiograptid approaching *L. retusus* Lapw.

It rather seems that forms such as the one here described, probably also some described as *Lasiograptus retusus* Lapw., are referable to the genus *Gymnograptus*. From typical lasiograptids they differ in the outline of apertural margin (straight) and in the septal list being more distinctly marked. Their general habitus of thecae and of rhabdosome come nearer to *Gymnograptus* than to *Lasiograptus*. This agrees with the opinion expressed by Dr. Strachan (*in litt.*).

The faunal assemblage associated with this form contain a great abundance of excellently preserved graptolites, by Prof. R. Kozłowski identified as *Mastigograptus* sp. No index form have, however, been recovered which would more definitely indicate the age of the boulder. Noteworthy is the occurrence in this assemblage of the hydroid *Rhabdohydra tridens* Kozł. which in boulder 0.94 is associated with *Gymnograptus linnarssoni*, and in boulder 0.26 — with *G. retioloides*. This hydroid, however, has a wide stratigraphic range, since it occurs also in assemblages suggestive of the Lower, Middle and Upper Ordovician. Hence it cannot supply evidence for determining the age of the boulder. *Lasiograptus retusus* Lapw., to which our form exhibits strongest resemblance, is known from the lower Llandeilo and the uppermost Llanvirn of Great Britain (Elles & Wood, 1901-1908, p. 329). This might possibly suggest its appearance at an earlier moment than that of the other gymnograptids. Together with its rather primitive structure, lacking specialization, this would be a feature reasonably leading to its recognition as a form closely allied with the ancestor of the other representatives of *Gymnograptus*.

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SYSTEMATIC POSITION OF GENUS *GYMNOGRAPTUS*

Better knowledge of the morphology of *Gymnograptus linnarssoni* (Moberg) which is the genoholotype of this genus and of related forms probably referable to the same genus, throws a new light on the systematic position of *Gymnograptus* Bulman.

Proximal thecae in *G. linnarssoni* and *G. retioloides* testify to their relationship with Lasiograptidae. The general appearance of thecae in *G. linnarssoni*, defined by Bulman as orthograptid, differs from the true orthograptid type and comes closer to thecae of Lasiograptidae. In a personal communication Dr. Jaanusson has made the suggestion to call this a "lasiograptid" type of thecae. These thecae differ, indeed, both from the orthograptid and the amplexograptid appearance. The ventral margin is nearly straight and strongly inclined to the axis of the rhabdosome. Very characteristic is likewise the elevation of the distal apertural margins of thecae. Together with the subapertural position of the ventral processes common in lasiograptids, this results in the characteristic appearance of the thecae.

During astogeny of *G. linnarssoni* the distinctly lasiograptid proximal thecae gradually pass into nearly orthograptid ones, i.e. with diminishing inclination of the ventral wall. The change of thecal shape is less distinctly marked in *G. retioloides*, but seems to be present. Still, the degree of inclination of the ventral thecal walls is smaller in all the studied representatives of *Gymnograptus* than it is in *Lasiograptus*, and resembles more the thecae in *Hallograptus*. The apertural parts of thecae, on the other hand, comes nearer to *Lasiograptus* than to *Hallograptus*.

Likewise, the rhabdosome section, nearly tabular, in result of the "reverse-obverse" flattening, brings *G. linnarssoni* and *G. retioloides* nearer to the Lasiograptidae, separating them from climacograptids whose rhabdosome sections are oval or circular (comp. fig. 6*B*, 17 *A*, *B*).

In arrangement of lists analogous with that in *Lasiograptus*, the structure of clathrium further confirms the similarity of the two above mentioned forms. The entirely closed abapertural rings in *G. retioloides* only are more strongly developed than those in the lasiograptids we know (*L. harknessi*, Bulman, 1947). Other gymnograptids in this respect resemble *L. harknessi* (comp. p. 322).

Bulman (1955, p. 87) referred *Gymnograptus* to "Diplograptidae *incertae sedis*". On a closer analysis of the here studied forms it seems that *Gymnograptus* is referable to the Lasiograptidae Bulman. This view is now shared by Prof. Bulman, Dr. Jaanusson and Dr. Strachan whose opinions seem notably reliable since they are the outstanding authorities on these problems and are in possession of comparative material (*in litt*).

Forms by the present writer referred to genus *Gymnograptus* probably represent somewhat divergent evolutionary trends. *Gymnograptus retioloides* comes closer to typical lasiograptids (structure of processes) than *G. linnarssoni*. These two forms may, however, be morphologically derivable from forms such as the here described *Gymnograptus* sp. in which some features of the both are combined. In thecal structure it resembles more *G. retioloides*, while its subapertural processes approach closer the very young processes of *G. linnarssoni*. The processes of both *G. retioloides* and *G. linnarssoni* are derivable from those of *Gymnograptus* sp. If the similarity of *Gymnograptus* sp. with *Lasiograptus retusus* is not deceptive, this hypothesis may be quite sound, inasmuch as there are data suggesting that this species made its first appearance somewhat earlier than the remaining gymnograptids. *G. linnarssoni* may be traced from such forms through modifications of thecal structure, progressive changes of budding and a reduction of the median septum. On the other hand, *G. retioloides* would seem to be more conservative in the astogeny and shape of thecae, and be characterized by progressive development of the subapertural processes. Certain similarities likewise exist between the thecae of *G. retioloides* and those of such climacograptids which have strongly developed ventral excavation and mesial process (*Climacograptus (Paraclimacograptus)* Přibyl). This gives their thecae a lasiograptid appearance. At present, however, it is hardly possible to determine how far this is an expression of the actual relationship or of convergence only.

The subapertural processes of *G. retioloides* do not resemble any processes in the Diplograptinae and the Climacograptinae known to the writer. Their bifurcation, however, as well as the subapertural position seems quite common in lasiograptids. Still it is not known to what extent these processes may constitute homologies of the ventral spines in other Lasiograptidae in which the "pelta" may likewise be supported by the spines. The mutual resemblance of these structures seems very strong.

In some points *G. retioloides* resembles Retiolitidae. This was noted by Wiman's quick eye (1895) who stressed it in its specific name. It applies particularly to the retiolitids which only have the clathrium but lack the reticula, since nothing suggests a tendency in *G. retioloides* to the formation of a reticula.

With respect to a general resemblance of the clathrium (arrangement of rods), (comp. fig. 15), *G. retioloides* doubtlessly comes closest to *Orthoretiolites* Whittington, by Bulman referred to the Retiolitidae (1955). Cardinal differences, however, exist between the here described form and *Orthoretiolites*, expressed by the mode of development (probably quite aseptal in *Orthoretiolites*), also by the structure of processes. Doubtlessly we are here dealing with parallelism between relatively distant phylogenetic lines.

Still closer resemblances supposedly exist between representatives of *Hallograptus* and *Orthoretiolites,* since the shape of thecae and the course of lists are strongly similar in both forms. Other retiolitids, i.e. *Holoretiolites* Eisenack, in the structure of processes approach *G. retioloides.* Notably similar processes are noted in *H. münchi.* In that form they are bifurcated, with the edges of the arcuately curved fuselli well marked (Eisenack, 1951, pl. 22, fig. 11, 12). In structural details these processes display differences: in *Holoretiolites* the basal portion is lacking and the arches are not attached to the lateral walls of theca.

In all probability, the mentoned similarities of structure may be interpreted as a parallelism in the development of the various characters, a phenomenon very common in graptolites.

Structure of *G. retioloides* resembles that of retiolitids in other characters too. An analysis of the structure of the proximal part of the clathrium in *G. retioloides,* sheds for example some light on the origin of an element so characteristic of Retiolitidae as the arrangement of rods in the "ancora" stage. Since the longitudinal rods of the prosicula are secondarily thickened, the virgula has in a certain sense a tendency for prolongation towards the prosicular aperture. In *G. retioloides* the virgella begins at approx. 0.2 to 0.3 mm from the prosicular aperture, while in some diplograptids, e.g. *Cl.* (= *Amplexograptus?*) *inuiti* Cox, it takes rise from the first metasicular fusellus. Hence we may readily reconstruct a complete hypothetical way of fusing the virgula with the virgella through longitudinal lists of prosicula. The structure thus formed would correspond to the "ancora" axis. The branches might possibly be formed by a similar mode of fusion of the ventral lists of th 1^1 and th 1^2, fused either directly or through one half of the apertural ring of metasicula (comp. fig. 15). Thus, this part of the clathrium in *G. retioloides* is built on a structural pattern essentially similar with that in Retiolitidae, though the two structures can hardly be considered as strictly homologous.

Differences of astogeny between *G. linnarssoni* and *G. retioloides* are conspicuous (comp. p. 319). It is, however, very difficult taxonomically to rank such differences. Most likely every diplograptid genus may include forms whose astogeny represents various, frequently very distinct modifications of diplograptid development (comp. differences in astogeny of *Cl. scharenbergi, Cl. diplacanthus* and *Cl. typicalis*). It seems that astogeny is very often a progressive character, showing even greater plasticity than the thecal structure (comp. progressive change in *Glyptograptus dentatus/teretiusculus* series, Bulman, 1936, p. 88, 89, and considerable differences in astogeny of *Climacograptus scharenbergi* which are most likely depended on geographic and zonal variation, Bulman, 1953, p. 511). Some stages of the diplograptid mode of development may be "reproduced" in phyletic lineages, with probably quite separate ancestry (comp. *"dentatus"* stage in *Glyptograptus* and *Dicranograptus,* Bulman, 1944, p. 40). In the light of these contradictory evidences the real taxonomic significance of the different modes of development needs further discussion. At the present moment we cannot define the taxonomic consequences of different changes in diplograptid development. The thecal structure must be considered as having rather greater practical significance. This is important insomuch that it is a feature persisting even in a flattened state of preservation. Hence the writer believes that on thecal structure *"Climacograptus" retioloides* Wiman may be provisionally referred to genus *Gymnograptus* (comp. p. 320).

HYPOTHETICAL RELATIONSHIPS WITHIN THE LASIOGRAPTIDAE

The assignment of genus *Gymnograptus* to the Lasiograptidae throws a new light on the supposed phylogenetic relations within that family. The knowledge of the morphology in *G. linnarssoni* and *G. retioloides* to a certain extent completes the picture of morphological differentiation of lasiograptids, as it has been presented in forms so far investigated (Elles & Wood, 1908; Elles, 1922; Bulman, 1932*a*, 1947, 1953, 1955; Jaanusson, 1959 — in print).

Genus *Gymnograptus* undoubtedly comes closest to *Lasiograptus*. Nevertheless, the thecal appearance of *Lasiograptus* differs from conditions noted in *Gymnograptus*, in that the thecae are provided with a deep oblique incision of apertural border and wide ventral excavation (comp. Bulman, 1947, pl. 8, fig. 11). *Gymnograptus linnarssoni* and *G. retioloides*, on the other hand, are characterized by only slight ventral excavation and by suspended apertural margin (comp. p. 293) due to the presence of "angular fuselli", lacking in representatives of *Lasiograptus*. The main character of thecae in *Lasiograptus* may, therefore, be defined as a modified amplexograptid type, associated with the presence of clathrium (comp. also Bulman, 1955, p. 87). The thecae in *Gymnograptus*, on the other hand, may by defined as modified diplograptid thecae, associated with the presence of clathrium. For *Gymnograptus linnarssoni* an astogenetic succession of thecae is highly characteristic, similar to that in *Diplograptus* McCoy — with amplexograptid (lasiograptid) proximal and nearly orthograptid distal thecae.

The position occupied by some forms is, however, intermediate as e.g. that of our *Gymnograptus* sp. and to some extent also *Gymnograptus retioloides*. In the former apertural margins are straight or only slightly suspended, but it also lacks the deep apertural incision, so characteristic of *Lasiograptus*. This form is close to *Lasiograptus retusus* Lapw.; shape of thecae, absence of a tendency to form lacinia, strong development of the septal list — these are all features reasonably suggesting the assignment of *Lasiograptus retusus* to *Gymnograptus*. A better knowledge of the structure of this graptolite is needed to decide its systematic position. Should this suggestion prove sound, genus *Lasiograptus* Lapw. would only retain forms exhibiting a common structural type of thecae and provided with more or less developed lacinium (e.g. *L. harknessi, L. costatus*).

Gymnograptus and *Lasiograptus* have many features in common, but differences in thecal structure and in the tendency to develop lacinia justify the opinion that they have separate ancestry.

Gymnograptus would then be regarded as presenting more primitive stage of specialization (development of clathrium, lack of lacinia). Should

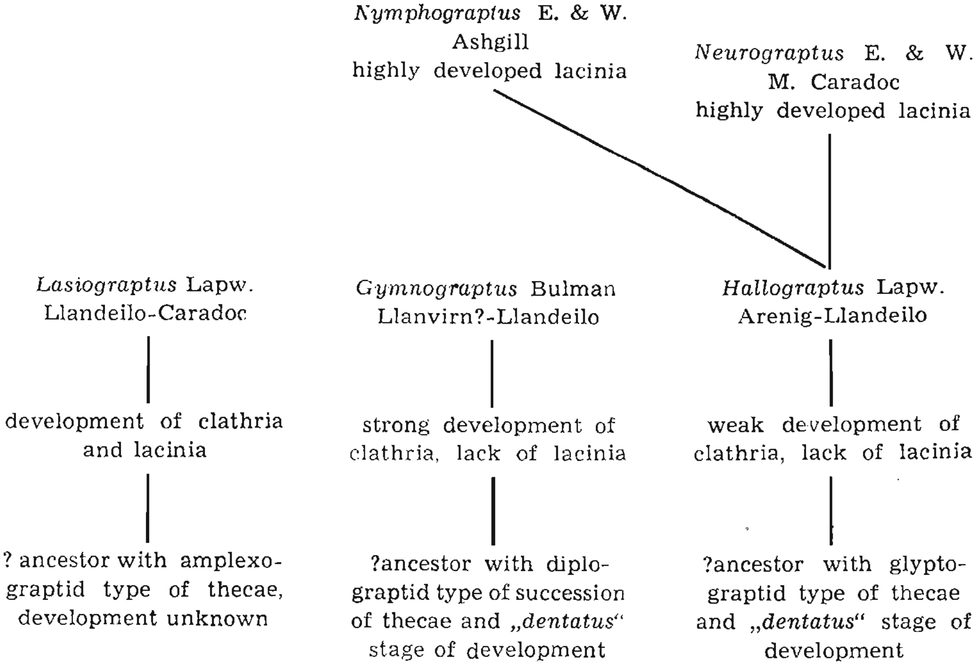
L. retusus be referred to *Gymnograptus* the stratigraphic range of this genus would stretch from the uppermost Llanvirn to the lower Llandeilo, while that of *Lasiograptus* s. str. — from the Llandeilo to the Caradocian. The latter would represent the more highly specialized group (comp. with diagram-tab. 6).

Gymnograptus, at least the line of *G. linnarssoni*, may be regarded as derivable from ancestors whose proximal thecae had a more or less "amplexograptid" appearance, while the distal ones were orthograptid, since this is the astogenetic succession encountered in *G. linnarssoni*. Their ancestor would then, on this ground, be referable to *Diplograptus* McCoy.

Lasiograptus s. str. represents the second trend (comp. diagram-tab. 6) with modified amplexograptid thecae, which suggests an amplexograptid ancestor. Evolution in this line was associated with development of clathrium and the tendency to form lacinia.

Table 6

Hypothetical relationships within the family Lasiograptidae Bulman



Into the Lasiograptidae would have to be included still another phylogenetic line, comprising *Hallograptus* Lapw., as well as genera *Neurograptus* Elles & Wood and *Nymphograptus* Elles & Wood, both approaching *Hallograptus* Lapw. in the shape of thecae (Bulman, 1955, p. 88). In what thecal structure is concerned, *Lasiograptus hystrix* Bulman is nearer to *Hallograptus* than to *Lasiograptus*[4]. Its development probably differs considerably from that of *L. harknessi* (Bulman, 1947). From typical hallograptids this form differs in introversion of lip of the ventral aperture of thecae, while the general thecal appearance resembles *H. mucronatus* (Hall), the genoholotype of *Hallograptus*. This thecal type may be regarded as approaching the glyptograptid in which pleural lists have developed and ventral spines have originated. Since the development of *L. hystrix* Bulman likewise assigned to genus *Hallograptus*, may be readily traced from *Glyptograptus dentatus* (Bulman, 1947) the writer supposes as probable the descent of that line from a glyptograptid ancestor with the "*dentatus*" type of development. Genus *Hallograptus*, here representing the lower evolution stage, occurs in the Llandeilo, while genera *Neurograptus* and *Nymphograptus* occur in the Middle Caradocian and the uppermost Caradocian or Ashgillian. The two last named genera are characteristic by progressive complication of the lacinium. Their structure and mutual relations have not been elucidated.

Some forms, tentatively referred to the Retiolitidae (Bulman, 1955, p. 88, 89), exhibit distinctly lasiograptid appearance. Among them is *Orthoretiolites*, in thecal shape resembling genus *Hallograptus*, also *Plegmatograptus* and *Pseudoplegmatograptus*, both provided with lacinia. The relation of these forms to the Lasiograptidae calls for further investigation.

According to the above considerations, the family Lasiograptidae probably form a heterogeneous assemblage which consists of at least three different trends having probably more or less separate ancestry. This agrees with Prof. Bulman's opinion that Lasiograptidae are probably an "unnatural" group (*in litt.*). The present author, however, believes that every future division of this group (if necessary!) needs better knowledge of all forms here under consideration. The views here mentioned may only be regarded as a working hypothesis. Although it may be deemed precocious in view of the meagre knowledge now available on the majority of forms here, still the writer ventures to suppose that the preparation of such work schemes may prove helpful in future discussion of the studied problems.

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[4] The writer's attention to this fact was called by Dr. Jaanusson.

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ADAM URBANEK

BADANIA NAD GRAPTOLITAMI

II. O ROZWOJU I BUDOWIE GRAPTOLITÓW Z RODZAJU *GYMNOGRAPTUS* BULMAN

Streszczenie

W pracy opisano astogenezę i morfologię *Gymnograptus linnarssoni* (Moberg) i *G. retioloides* (Wiman) oraz fragment rabdozomu *Gymnograptus* sp. Materiał wypreparowano z pięciu głazów narzutowych wieku środkowo-ordowickiego, pochodzenia skandynawskiego.

Gymnograptus linnarssoni (Moberg) jest charakterystyczną formą dla dolnej części środkowego ordowiku Bałtoskandii. Jednakże dotychczas nie poznano dokładnie budowy i rozwoju tego graptolita, gdyż znany był jedynie w stanie spłaszczonym, lub wypreparowany był ze skał ze zbyt silnie zwęgloną perydermą. Na podstawie okazów znalezionych w Polsce (głazy 0.94 i 0.96 z Jarosławca, Pomorze Zachodnie) gatunek ten można określić jako graptolita biserialnego z tekami proksymalnymi, zbliżonymi do lasiograptusowych, dystalnymi zaś — prawie ortograptusowymi. Pierwsze dwie teki pozbawione są wyrostków aperturalnych, następne opatrzone są kolcami subaperturalnymi, podwójnymi lub potrójnymi, o bardzo zmiennym kształcie. Krawędzie tek tworzą silne zgrubienia perydermy, dające w rezultacie rodzaj clathrium, na którym rozpięta jest ścieniała błona perydermalna. Sikula opatrzona jest wirgellą i kolcem dorsalnym. Rozwój diplograptidowy; cztery lub pięć pierwszych tek alternuje, pozostałe począwszy od tek 3^1 i 3^2 tworzyły dwie niezależne serie. Jednakże septum medialne, we właściwym tego słowa znaczeniu, tu nie istnieje; brak bowiem błony perydermalnej, rozdzielającej obie serie tek. Wirgula przytwierdza się do rabdozomu przy pomocy beleczek, mających kształt litery „U" i stanowiących odpowiedniki pierścieni abaperturalnych. Budowa taka odpowiada formom septalnym; ponieważ jednak właściwego septum brak, proponuję zastosować tu termin „kryptoseptum".

Gymnograptus retioloides (Wiman) nie jest znany „in situ", a poprzednio opisany był na podstawie fragmentarycznego okazu, pochodzącego z głazu narzutowego (Wiman, 1895). Obecnie, na podstawie materiału wypreparowanego z dwu głazów narzutowych (0.26 i 0.31 z przedmieścia Poznania — Czerwonak), można było wyjaśnić jego astogenezę i budowę. Jest to graptolit biserialny, z tekami zbliżonymi do typu lasiograptusowego. Pierwsze dwie teki opatrzone są nieparzystymi kolcami subaperturalnymi, pozostałe — rozdwojonymi wyrostkami subaperturalnymi w postaci podwójnej pętli, na której rozpięta jest cienka błona perydermalna. Clathrium silnie rozwinięte, peryderma natomiast cienka. Sikula opatrzona tylko wirgellą, rozwój diplograptidowy septalny. Pięć pierwszych tek alternuje; pączkowanie tek 1^1 i 1^2 oraz 2^1 i 2^2 — jak w stadium „*dentatus*", lecz zarówno teka 3^1, jak i 3^2 powstają z teki 2^2. Gatunek ten zaliczony był przez Wimana do rodzaju *Climacograptus* Hall. Różni się jednak od klimakograptusów budową tek, obecnością clathrium, przekrojem rabdozomu i budową wyrostków. Najwięcej cech zdaje się zbliżać go do *Gymnograptus* Bulman, choć i tu występują dość znaczne różnice w typie rozwoju i budowie wyrostków subaperturalnych. Być może różnice te można by uznać za wystarczające dla ustanowienia nowego podrodzaju lub rodzaju. Autor jednak uważał za stosowne zaliczyć tę formę prowizorycznie do *Gymnograptus*, kierując się ogólnym pokrojem rabdozomu i kształtem tek oraz unikając tworzenia monotypowej jednostki taksonomicznej.

Gymnograptus sp. opisany został na podstawie tylko jednego fragmentu części dystalnej rabdozomu (głaz 0.181 z Mocht, 40 km NW od Warszawy). Zbliża się on do *Lasiograptus retusus* Lapworth i może być nawet identyczny z nim gatunkowo.

Do rodzaju *Gymnograptus* Bulman, dotychczas monotypowego, należy — zdaniem autora — zaliczyć obecnie także „*Climacograptus*" *retioloides* Wiman i prawdopodobnie „*Lasiograptus*" *retusus* Lapworth. Rodzaj ten winien być zaliczony do rodziny Lasiograptidae Bulman, w obrębie której stanowi prawdopodobnie ogniwo cechujące się niższym stopniem specjalizacji, niż *Lasiograptus* Lapworth. Przypuszczenie to opiera autor na analizie porównawczo-anatomicznej opisanych form i innych dotychczas poznanych graptolitów, należących do zbliżonych grup systematycznych.

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 282)

Gymnograptus linnarssoni (Moberg), młoda metasikula z fragmentem prosikuli, *vi* wirgella; ca. × 62 (głaz 0.94).

Fig. 2 (p. 282)

Gymnograptus linnarssoni (Moberg), metasikula z pączkiem pierwotnym i otworem dla pączka 1^2, *A* od strony „reverse", *B* od „obverse"; ca. × 62 (głaz 0.94).

Fig. 3 (p. 283)

Gymnograptus linnarssoni (Moberg), budowa fuzellarna proksymalnej części rabdozomu, strona „reverse"; *vi* wirgella, *ds* kolec dorsalny; ca. × 50 (głaz 0.94).

Fig. 4 (p. 284)

Gymnograptus linnarssoni (Moberg), budowa fuzellarna proksymalnej części rabdozomu od strony „reverse"; *vi* wirgella, *ds* kolec dorsalny, *r* przypuszczalnie zregenerowana część perydermy; ca. × 50 (głaz 0.96).

Fig. 5 (p. 285)

Gymnograptus linnarssoni (Moberg), budowa fuzellarna proksymalnej części rabdozomu od strony „obverse". Okaz, powiększenie i objaśnienia — jak fig. 4.

Fig. 6 (p. 287)

Diagram uwidoczniający granice i wzajemne stosunki topograficzne tek oraz stosunek wirguli do rabdozomu u *Gymnograptus linnarssoni*: *A* proksymalna część rabdozomu od strony „reverse", *B* schematyczny widok od góry przedstawiający stosunek wirguli do septum intertekalnego. Granice tek na stronie przeciwnej zaznaczono liniami przerywanymi; *v* wirgula, *abp* pierścień abaperturalny, ca. × 25.

Fig. 7 (p. 287)

Diagram uwidoczniający granice i wzajemne stosunki topograficzne tek oraz stosunek wirguli do rabdozomu u *Gymnograptus linnarssoni*, widziane od strony „obverse". Granice tek na stronie przeciwnej zaznaczono liniami przerywanymi; *v* wirgula, *abp* pierścień abaperturalny, *ap* listewka aperturalna, *pl* listewki pleuralne, *sept* listewki septalne; ca. × 25.

Fig. 8 (p. 288)

Rekonstrukcja przypuszczalnego sposobu pączkowania u *Gymnograptus linnarssoni* (Moberg).

Fig. 9 (p. 292)

Gymnograptus linnarssoni (Moberg), bardziej dystalna część rabdozomu, widziana lateralnie; ca. × 50 (głaz 0.94).

Fig. 10 (p. 293)

Gymnograptus linnarssoni (Moberg), budowa fuzellarna jednej z tek bardziej dystalnych, okaz — jak fig. 9 i pl. I, fig. 2; *ap* listewka aperturalna, *p* wyrostek subaperturalny, *par* listewka parietalna, *pl* listewka pleuralna, *sept* listewka septalna; ca. × 58 (głaz 0.94).

Fig. 11 (p. 293)

Gymnograptus linnarssoni (Moberg), budowa fuzellarna ścianki wentralnej teki; *bp* nasada wyrostków subaperturalnych, *pl* listewki pleuralne; ca. × 92 (głaz 0.96).

Fig. 12 (p. 295)

Gymnograptus linnarssoni (Moberg), budowa fuzellarna nasadowej części wyrostka subaperturalnego, uproszczone, części rekonstruowane zaznaczono liniami przerywanymi; ca. × 116 (głaz 0.94).

Fig. 13 (p. 305)

Diagram ilustrujący sposób pączkowania tek u *Gymnograptus retioloides* (Wiman).

Fig. 14 (p. 305)

Stosunek między tempem pączkowania pierwszej i drugiej serii rabdozomu *Gymnograptus retioloides* (Wiman); *v* wirgula, *vi* wirgella, *ms* septum medialne. Oparte na okazie pl. I, fig. 3.

Fig. 15 (p. 311)

Budowa clathrium u *Gymnograptus retioloides* (Wiman), diagram oparty na konkretnym okazie; *am* pierścień apertury sikuli, *abp* pierścień abaperturalny, *ap* listewka aperturalna, *bp* część nasadowa wyrostków, *par* listewki parietalne, *pl* listewki pleuralne, *sept* listewka septalna, *th. cc* zgrubienie wokół kanału krzyżującego teki 2^1, *v* wirgula, *vi* wirgella, *vl* listewka wentralna, ca. × 25.

Fig. 16 (p. 314)

Gymnograptus retioloides (Wiman), budowa fuzellarna septum medialnego teki 4^1; *ov* strona „obverse", *rv* strona „reverse", *s* krawędź proteki i septum medialnego, *si* sikula, *abp* odpowiednie pierścienie abaperturalne, *v* wirgula; ca × 93 (głaz 0.31).

Fig. 17 (p. 315)

A schematyczny przekrój poprzeczny rabdozomu *Gymnograptus retioloides* (Wiman), oparty na rabdozomie widzianym od góry, *B* to samo u *Climacograptus* cf. *scharenbergi*; *abp* pierścień abaperturalny, *v* wirgula; ca. × 25.

Fig. 18 (p. 322)

Gymnograptus sp., *A* fragment rabdozomu widziany lateralnie, *B* schematyczny fragment septum medialnego, *C* wyrostek subaperturalny widziany od góry; ca. × 25 (głaz 0.181).

Text-pl. I (p. 296)

Gymnograptus linnarssoni (Moberg), zmienność postaci wyrostków subaperturalnych; *1-3* tek proksymalnych: *1* wolna część wirgelli, *2, 3* wyrostki tek 2^1 i 2^2; *4-8* tek dystalnych: 4 zawiązek wyrostka subaperturalnego; ca. × 76 (głazy 0.94 i 0.96).

Text-pl. II (p. 300)

Gymnograptus retioloides (Wiman), rozwój sikuli i pączkowanie pierwszej teki: *1* prosikula bez żeberek podłużnych, ca. × 95; *2* prosikula z żeberkami podłużnymi, ca × 95; *3* młoda metasikula widziana z dwu stron (*a*, *b*), ca. × 125; *4* bazalna część wirgelli, ca. × 145; *5* sikula z pierwszą teką, *a* od strony „reverse", *b* wentralnie, *c* od strony „obverse", ca. × 47,5 (*1-3* głaz 0.26, *4-5* głaz 0.31).

Text-pl. III (p. 302)

Gymnograptus retioloides (Wiman): *1*, 2 pączkowanie tek 2^1 i 2^2 od strony „reverse"; *cc* kanał krzyżujący teki 2^1, *si* sikula; ca. × 63 (głaz 0.31).

Text.-pl. IV (p. 304)

Gymnograptus retioloides (Wiman), młody rabdozom w stadium czterech tek: *A* od strony „reverse", *B* od strony „obverse", *n* wnęka dla septum intertekalnego teki 3^1, *v* wirgula, *vi* wirgella; ca. × 50 (głaz 0.26).

Text-pl. V (p. 306)

Gymnograptus retioloides (Wiman), budowa fuzellarna proksymalnej części rabdozomu, uproszczona; części zrekonstruowane zaznaczono liniami przerywanymi: *A* od strony „reverse", *B* od strony „obverse"; ca. × 50 (głaz 0.31).

Text-pl. VI (p. 309)

Gymnograptus retioloides (Wiman), budowa fuzellarna tek, *1* teka 7^1 widziana lateralnie, drobnych szczegółów perydermy nie uwzględniono, ca. × 50; *2* teka widziana wentralnie, widoczna budowa septum intertekalnego, ca. × 98; *3* teka widziana lateralnie, budowa nieco inna niż na fig. 1, ca. × 50; *4* apertura teki 6^2 z fuzellusami kątowymi, *am* krawędź apertury, *a* łuki wyrostków, *ax* część osiowa wyrostka, *iths* septum intertekalne, ca. × 90 (głaz 0.31).

Text-pl. VII (p. 312)

Gymnograptus retioloides (Wiman), budowa wyrostków subaperturalnych, *1* teki *n* (3 lub 4), *a* od góry, *b* lateralnie, ca × 115; *2* teki (*n*+4), *a* od góry, *b* lateralnie, ca. × 115; *3* zawiązek wyrostka subaperturalnego teki 1^1, ca. × 270 (okaz — jak Text-pl. II, fig. 5); *4* budowa fuzellarna wyrostka teki 1^2, ca. × 270 (okaz — jak Text-pl. III, fig. 1), (głaz 0.31).

Pl. I

Fig. 1, 2. *Gymnograptus linnarssoni* (Moberg), *1* proksymalna część rabdozomu, strona „reverse" (głaz 0.96, Jarosławiec), *2* środkowa część rabdozomu, okaz nieco bardziej uszkodzony niż na fig. 9 (głaz 0.94, Jarosławiec); ca. × 25.

Fig. 3. *Gymnograptus retioloides* (Wiman), proksymalna część rabdozomu, strona „reverse", widoczne nierówności perydermy (głaz 0.31, Poznań-Czerwonak); ca. × 25.

Fig. 4. Fragment septum medialnego u *Climacograptus* sp., widoczna wypadająca błona perydermalna (wyspa Öland, Seby, „Schroeteri" Limestone); ca. × 37,5.

Pl. II

Gymnograptus retioloides (Wiman)

Fig. 1. Proksymalna część rabdozomu, strona „reverse"; ca. × 25.

Fig. 2. Ten sam okaz, strona „obverse"; ca. × 25.

Fig. 3. Wypreparowany wyrostek subaperturalny, widziany od góry: ca. × 62,5.

Fig. 4-7. Mikrotomowe przekroje poprzeczne wirguli: *4, 5* prawdopodobnie fragment bardziej proksymalny i młodszy; *6, 7* prawdopodobnie fragment bardziej dystalny i starszy; ca. × 1000. Przekroje *4, 6, 7* — grubości 5 μ, przekrój *5* — grubości 6 μ.

(Głaz 0.31, Poznań-Czerwonak).

АДАМ УРБАНЭК

О РАЗВИТИИ И СТРОЕНИИ ГРАПТОЛИТОВ РОДА *GYMNOGRAPTUS* BULMAN

Резюме

В работе дано описание астогенеза и морфологии *Gymnograptus linnarssoni* (Moberg) и *Gymnograptus retioloides* (Wiman), а также фрагмента рабдосомы *Gymnograptus* sp. Материал отпрепарирован из пяти валунов, сложенных среднеордовикскими известняками скандинавского происхождения.

Gymnograptus linnarssoni (Moberg) является характерной формой для нижней части среднего ордовика Балтоскандии. Однако до сего времени не было установлено точное строение и развитие этого граптолита, известного единственно в виде сплющенном, а если отпрепарированном из породы, то с сильно обугленной перидермой. Основываясь на образцах найденных в Польше (валуны 0.94

и 0.96 из Ярославца, Западное Поморье), граптолиты принадлежащие к этому виду можно определить как бисерийные, с проксимальными теками близкими к ласиограптусовым, и с почти ортограптусовыми дистальными. Первые две теки лишены апертурных отростков, следующие снабжены двойными или тройными субапертурными шипами очень изменчивой формы. Перидерма на краях тек сильно утолщена, образуя clathrium, на котором растянута утонченная перидермальная перепонка. Сикула снабжена виргеллей и дорсальным шипом. Развитие диплограптидовое. Первые четыре-пять тек расположены вперемежку; остальные же, начиная с тек 3^1 и 3^2, образуют две независимые серии. Однако медиальная перегородка (septum), в собственном этого слова значении, отсутствует, так как нет перидермальной перегородки разделяющей обе серии тек. Виргула прикрепляется к рабдосоме посредством балочек в виде буквы „U", представляющих собой эквивалент абапертурных колец. Такое строение соответствует формам септальным, однако ввиду отсутствия истинной септы предлагается применить в данном случае термин „cryptoseptum".

Gymnograptus retioloides (Wiman) не известен „in situ", а раньше был описан на основании фрагментарного образца из валуна (Wiman, 1895). Сейчас, на основании материала отпрепарированного из двух валунов (0.26 и 0.31 из предместья города Познань-Червонак), можно выяснить его астогенез и строение. Является он бисерийным граптолитом с теками, приближающимися к типу ласиограптусовому. Первые две теки снабжены непарными субапертурными шипами, прочие — раздвоенными субапертурными отростками в виде двойной петли, на которой растянута тонкая перидермальная перепонка. Clathrium сильно развит. Перидерма тонкая. Сикула снабжена только виргулой; развитие диплограптидовое — септальное; альтернирует пять первых тек, почкование тек 1^1 и 1^2, а также 2^1 и 2^2 как в стадии „*dentatus*", но теки 3^1 и 3^2 почкуют из теки 2^2. Вид этот отнесен был Виманом к роду *Climacograptus* Hall. От климакограптусов отличается однако строением тек, присутствием clathrium, очертанием разреза рабдосомы и строением отростков. Большинство признаков приближает его повидимому к *Gymnograptus* Bulman, хотя и тут существуют довольно значительные отличия в типе развития и в строении субапертурных отростков. Может быть, что различия эти могут быть признаны достаточными для выделения нового рода или подрода. Однако автор считает уместным отнести эту форму предварительно к *Gymnograptus* руководствуясь общим покроем рабдосомы и формой тек, а также во избежание установления монотипной таксономической единицы.

Gymnograptus sp. описан на основании только одного фрагмента (из валуна 0.181 из Мохт, 40 км NW от Варшавы) дистальной части рабдосомы. Приближается он к *Lasiograptus retusus* Lapworth и может быть даже с ним тождественным. Согласно мнению автора, к монотипному до сих пор роду *Gymnograptus* Bulman следует отнести также „*Climacograptus*" *retioloides* Wiman, а возможно что и „*Lasiograptus*" *retusus* Lapworth. Этот род следует отнести к семейству Lasiograptidae Bulman, среди которого составляет он по всей вероятности эволюционное звено, отличающееся более низким уровнем специализации по сравнению с *Lasiograptus* Lapworth. Это предположение обосновывает автор сравнительно анатомическим анализом описанных форм и других изученных до настоящего времени граптолитов, относящихся к близким систематическим группам.

EXPLANATION OF PLATES

Pl. I

Fig. 1, 2. *Gymnograptus linnarssoni* (Moberg). *1* proximal part of rhabdosome, reverse side (boulder 0.96, Jarosławiec), *2* medial part of rhabdosome, lateral view, specimen somewhat more damaged as compared with text-fig. 9 (boulder 0.94, Jarosławiec); ca. × 25.

Fig. 3. *Gymnograptus retioloides* (Wiman), proximal part of rhabdosome, reverse side, showing roughnesses of periderm (boulder 0,31, Poznań-Czerwonak); ca. × 25.

Fig. 4. Fragment of the median septum in *Climacograptus* sp. showing peridermal membrane just falling out (Öland, loc. Seby, "Schroeteri" Limestone); ca. × 37,5.

Pl. II

Gymnograptus retioloides (Wiman)

Fig. 1. Proximal part of rhabdosome, reverse side; ca. × 25.

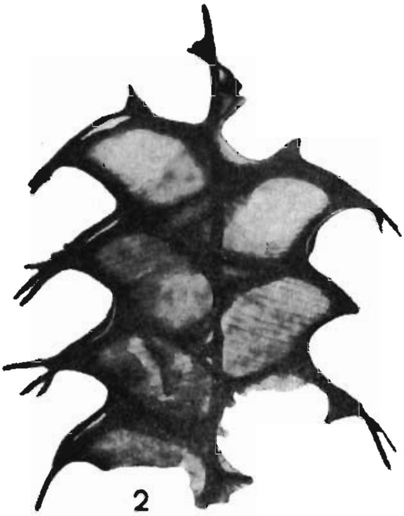
Fig. 2. Ditto, obverse side; ca. × 25.

Fig. 3. Isolated subapertural process, top view; ca. × 62,5.

Fig. 4—7. Microtome cross sections of virgula: *4*, *5* probably more proximal and younger fragment; *6*, *7* probably more distal and older fragment; ca. × 1000. Sections *4*, *6*, *7* — cut at 5μ, section *5* — cut at 6μ.

(Boulder 0.31, Poznań-Czerwonak).


4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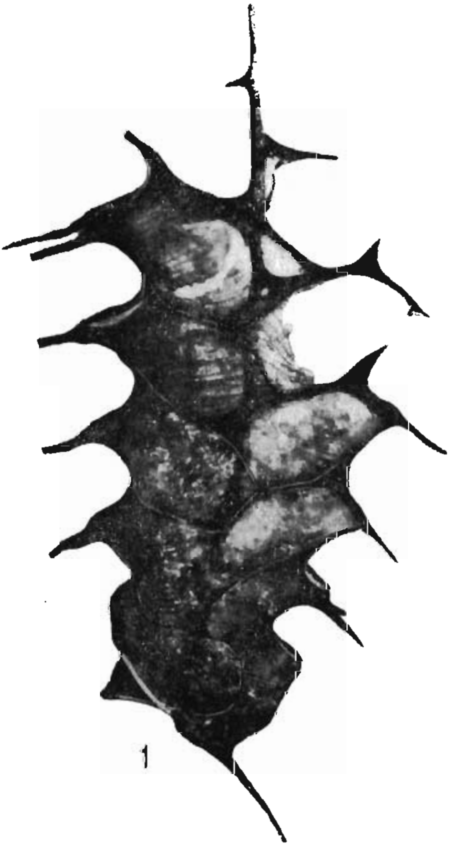
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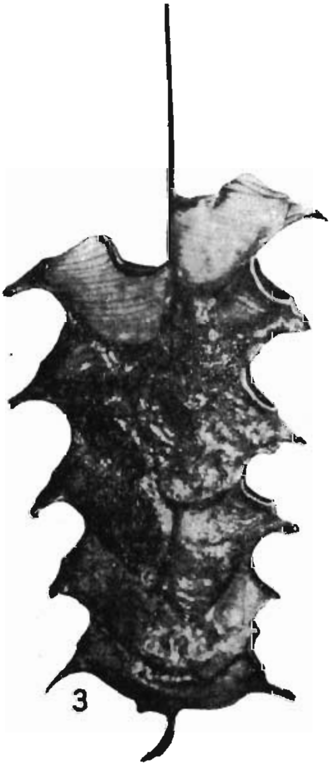
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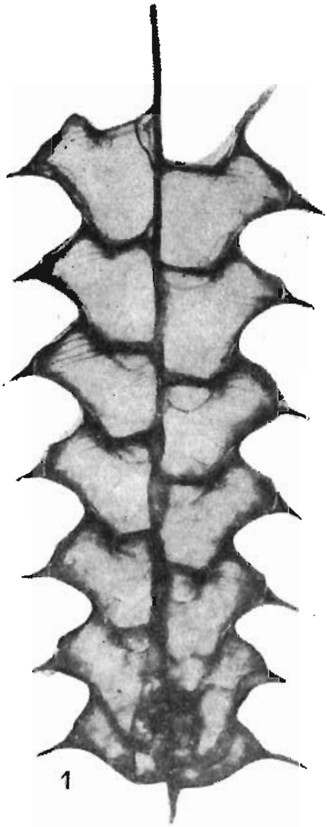
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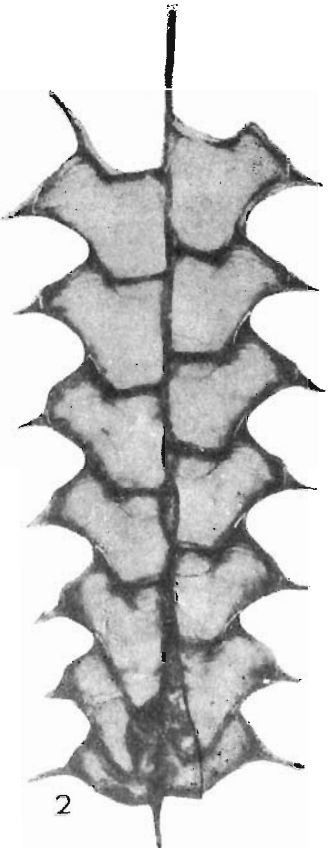
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